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DINOSAUR TRACKWAYS IN THE WINTON FORMATION (MID-CRETACEOUS) OF QUEENSLAND

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ABSTRACT

Dinosaur trackways have been discovered at several closely-grouped sites in mid-Cretaceous sediments of the Winton Formation, central W. Queensland. At one of these sites about 209 m^2 of bedding plane was exposed to reveal trackways of more than 150 bipedal dinosaurs. One of these trackways is very much larger than any of the others; it is attributed to a large theropod dinosaur (carnosaur) and is identified as cf. *Tyrannosauropus.* The remaining trackways are referred to two new ichnotaxa — *Wintonopus latomorum* and *Skartopus australis* — which are attributed to ornithopods and coelurosaurs (respectively). The sizes of the track-makers are estimated by means of allometric equations derived from osteological data; the speeds of the track-makers are estimated by using the mathematical relationships of size, speed and gait that have been determined for living tetrapods. The carnosaur is estimated to have been about 2.6 m high at the hip, and to have been walking at a speed of about 7 km/h. The ornithopod track-makers ranged from 14 to 158 cm in height at the hip; these animals were using a fast running gait equivalent to cantering or galloping in mammals, and their mean speed is estimated at 16 km/h. The coelurosaur track-makers ranged from 13 to 22 cm in height at the hip; these too were using a fast running gait, and their mean speed is estimated to have been 12 km/h. The trackways of the ornithopods and coelurosaurs are interpreted as those of animals caught up in a stampede — which was presumably triggered by the approach of the carnosaur. It is suggested that relative stride length (i.e. stride length relative to height at the hip) is the best available criterion for appraising the locomotor performances of dinosaurian track-makers. By this criterion the performances of the Winton ornithopods and coelurosaurs are outstandingly good. There is an indication that these animals were running at or near their maximum speeds — with relative stride lengths in the range 3.9 to 5.0. If the most highly adapted of cursorial dinosaurs (the ornithomimids or 'ostrich dinosaurs') attained such figures for relative stride length their speeds would have been up to about 60 km/h.

INTRODUCTION

In June 1976 Mr Ron McKenzie showed us some well-preserved dinosaur footprints that he had collected from a site about 120 km SW of Winton, central west Queensland. The footprint site, which was later named Seymour Quarry, was in sediments of the Winton Formation (mid-Cretaceous) and its existence was known to many residents in the Winton area. In 1971 a small field party including Dr R.H. Tedford (American Museum of Natural History) and Dr A. Bartholomai (Queensland Museum) paid a brief visit to the site; this party established that the footprint horizon extended to a second site some 100 metres away (Knowles 1980). This second site, which was later named Lark Quarry, subsequently proved to be of very great interest.

The footprints at these localities attracted our attention because of their abundance, their excellent preservation and their remarkably small size (by dinosaurian standards). In 1976 we carried out preliminary excavations at both sites, and in the following year a large labour-force of volunteers co-operated in a major excavation at Lark Quarry. This excavation revealed several thousands of footprints representing the trackways of well over 100 bipedal dinosaurs — many of them apparently no bigger than chickens. In preliminary accounts the Lark Quarry trackways have been interpreted as evidence of a dinosaur stampede (Thulborn and Wade 1979, Wade 1979). If this interpretation is correct it may carry important implications for current understanding of dinosaur biology. The present work has three aims: 1) to provide a systematic account of the trackways at Lark Quarry and its surroundings; 2) to offer some interpretations regarding the sizes, speeds and behaviour of the track-makers; 3) to justify those interpretations and to consider their implications for the understanding of dinosaur biology.

LOCALITIES

The footprints described in this paper were found at three localities on Mt Cameron property, SW of the town of Winton in central west Queensland. About 95 km SW of Winton the road to Jundah and Stonehenge runs along the crest of a west-facing scarp (the Tully Range) which is formed by sediments of the Winton Formation capped by duricrust. The localities are close to the foot of the scarp, alongside a track leading NW to Cork Station. The maximum distance between any two of the localities is about 200 m (see map, Fig. 1).

Seymour Quarry. A deep hillside cutting alongside the track to Cork Station. The site is identified as an opal mine on the Brighton Downs sheet of the BMR 1:250,000 series of geological maps (sheet SF/54-15; map reference 23°01'S, 142°24'W). Footprints occur as natural casts below a thin bed of red arkosic sandstone that outcrops at the foot of the hill. This friable sandstone overlies a weathered mudstone, and its lower surface is infiltrated by dark brown ironstone which prevents the footprints from crumbling on exposure. Traces of plant rootlets are preserved along with the footprints, while these themselves are very well preserved and may even show indications of skin texture (see p. 422, Pl. 1). The footprints are attributed to small bipedal dinosaurs of two types (coelurosaurs and ornithopods), and they appear to represent continuations of trackways at another site to the SW (Lark Quarry). This first site is named for Mr Glen Seymour, its discoverer and former manager of Cork Station.

Lark Quarry (Pl. 3). A large excavation revealing more than 200 m^2 of a single bedding plane. This site is located to the SW of Seymour Quarry, and has been the subject of preliminary descriptions (Thulborn and Wade 1979, Wade 1979). The Lark Quarry bedding plane carries well over 3000 footprints, representing the trackways of at least 150 bipedal dinosaurs. The trackways are almost entirely unidirectional: one track-maker was headed to the SW, whereas all the others were headed to the NE (in the direction of the present Seymour Quarry). The footprints occur as natural moulds in a bed of laminated claystone which varies between 6 and 12 cm in thickness. The footprint itself will be referred to as a mould, and the filling of the footprint as a cast, in conformity with standard ichnological usage. The claystone is generally bright pink in colour (though individual laminae range from pink through red to purple), and its upper surface appears to be stained dark red-brown by ironstone infiltration. This 'surface stain' is in fact an extremely thin adhesion from the base of the overlying sandstone. Below the claystone is a thick bed of arkosic sandstone; this is buff in colour and finely cross-bedded. Similar sandstone/claystone couplets occur above and below the trackway horizon. The next claystone bed below the trackway horizon also bears footprints in the form of natural moulds, though these are uncommon and seem to have no preferred orientation. The footprint horizon at Seymour Quarry seems to be an extension of the main trackway surface at Lark Quarry; it is possible to trace the footprint horizon through intermediate outcrops, though there is a complete break of about 30 metres caused by a creek bed. Moreover there is a uniform dip to the NW of about 4°, and by taking direct line of sight along the Lark Quarry bedding plane this will be found to coincide with the footprint horizon at Seymour Quarry. It may be mentioned that the reverse procedure (extrapolating the dip of the beds at Seymour Quarry) was used to locate the Lark Quarry trackways in the first instance (Knowles 1980). At both sites the footprints are similar in diversity, in abundance, in morphology and in their singular orientation. Lark Quarry has been designated an Environmental Park by the National Parks and Wildlife Service, Queensland, and is now roofed for its protection. The site is named for Mr Malcolm Lark, of Miles, who played a leading role in its excavation.

New Quarry. One of a series of small hillside exposures scattered from 100 to about 120 m due S of Lark Quarry. At the New Quarry site the trackway of a single bipedal dinosaur was measured *in situ*. In its preservation this trackway is identical to those at Lark Quarry. There is a major erosional gap between New Quarry and Lark Quarry, but at both sites the footprints occur at equivalent levels in similar sequences of sandstone/claystone couplets. Moreover at both

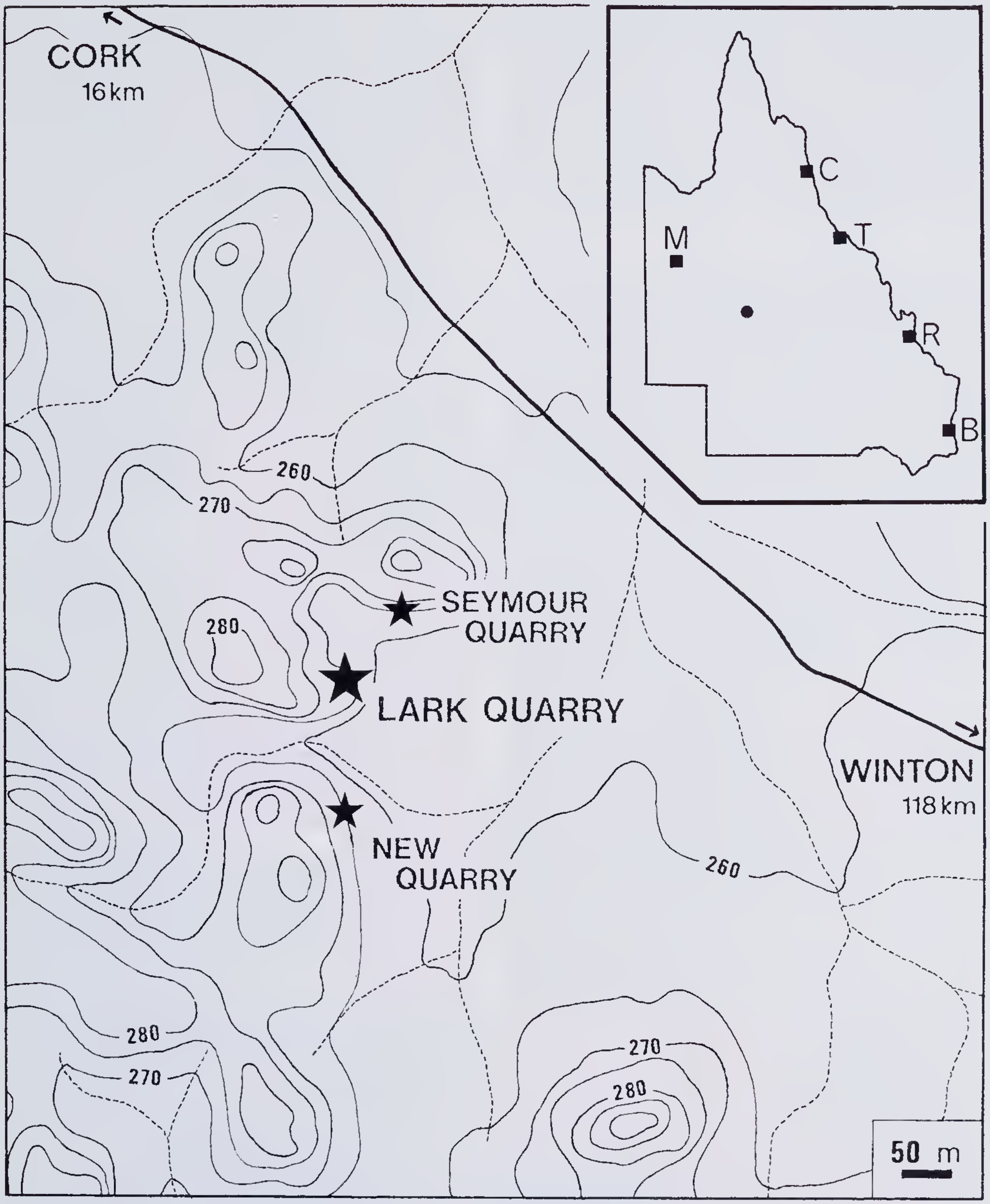

FIGURE 1. Map showing location of footprint sites. Contours are at 5 m intervals, and dashed lines indicate dry creek-beds. Inset map shows location of quarry in Queensland. B, Brisbane; C, Cairns; M, Mt. Isa; R, Rockhampton; T, Townsville.

sites there is a marked change in sediment type about 5 or 6 m above the footprints — the appearance of a yellowish arkose containing scattered plant fragments. The evidence is not conclusive, but it suggests that the New Quarry trackway is at about the same stratigraphic level as the Lark Quarry trackways. Footprints also occur in the next claystone layer below the New Quarry trackway; at this lower level the claystone is thoroughly trampled and churned up by deep footprints without preferred orientation.

METHODS

Excavation and collection of footprints

At Seymour Quarry the footprint horizon was reached by digging through the overburden of soil and weathered rock. The thin sandstone layer bearing the footprints (natural casts) proved rather fragile; most footprints collected from this site are on small slabs or are in the form of detached casts (see Pl. 1). One large slab (QM F12266) is approximately 95 by 40 cm and carries casts of at least 28 footprints — representing about 19 trackways.

At Lark Quarry the footprints were exposed by breaking up and removing a thick overburden of sandstone. Fortunately the sandstone was well jointed (as is the footprint surface — see Pl. 4), and it could be removed in blocks once these had been levered out with crowbars and jack-hammer. About 60 tons of overburden was removed, exposing an area of more than 209 m^2. It was then necessary to clean the footprints (natural moulds) be removing the sandstone that filled them. This sandstone filling was soft enough to be broken up with an awl. At the bottom of each footprint mould the colour of the sandstone filling changed from orange-red to bright yellow-green — a useful guide to ensuring that the footprints were fully excavated. More than 3300 footprints were exposed and cleaned in this way. A portion of the footprint bed was removed from the eroded NE margin of the site and was transferred to the Queensland Museum (QM F10321). In addition several individual footprints were collected — including holotypes of the new ichnotaxa described below.

Fibreglass replicas

After the Lark Quarry bedding plane had been exposed, and its footprints were thoroughly excavated, it was swept free of dust and rock debris; large parts of the bedding plane were then coated with liquid latex, which was reinforced with a cloth backing. Once it had set, the latex was stripped off in the form of large 'peels' (Wade 1979). These latex 'peels' were later used as a basis for moulding a fibreglass replica of the bedding plane and its footprints. The entire area shown in Fig. 3 was included in this replica. Individual footprints were also replicated (see, for example, Pl. 5, Fig. A). These high-fidelity replicas are much lighter and more durable than plaster casts; they enabled us to undertake a long-term study of the Lark Quarry footprints, even though our total expenditure of time at the site was no more than a few weeks.

Illustrations

The Lark Quarry bedding plane is almost horizontal, and its footprints are under natural low-angle lighting for only a few minutes after dawn and before dusk. Even at these times of day it may be difficult to obtain worthwhile photographs because the direction and intensity of lighting cannot be adjusted. We obtained few good quality photographs of individual footprints *in situ*. Most of our illustrations (Pl. 5 to 16) show fibreglass replicas of the footprints — though some do show original material (including type specimens; see plate captions).

Most of the area exposed at Lark Quarry was marked out with a grid of chalk lines, and each quadrat was photographed from a height of 1 metre (with the camera mounted on a rigid iron frame). The resulting photographs were then assembled into an accurate and detailed photomosaic — a representative portion of which is reproduced as Pl. 4. The same photographs were later used in drawing up a chart to show the distribution of footprints at Lark Quarry (Pl. 17).

Descriptions

There are no universally accepted methods for describing footprints and trackways (Sarjeant 1975, Leonardi 1979a), and it is necessary to define the measurements and statistics we employ. All linear measurements are expressed in centimetres.

Footprint length (abbreviation FL) — the maximum footprint dimension measured along, or parallel to, the axis of the longest digit (see Figs. 2A, B).

Footprint width (FW) — the maximum footprint dimension measured at a right angle to footprint length (Figs. 2A, B).

The ratio *footprint width / footprint length* (ratio FW/FL) is used to express footprint proportions.

We discovered that FL and FW were quite variable within each trackway, so that neither of these measurements could be regarded as a completely reliable indicator of the track-maker's size. Consequently we calculated an *index of footprint size* (SI) for each footprint:

$$SI = (FL \times FW)^{0.5}$$

This index was found to be remarkably consistent within each trackway, and it seems to be a useful guide to the relative sizes of two or more track-makers. The index is expressed in centimetres.

Interdigital angles (expressing divarication of digits) are commonly cited in descriptions of vertebrate footprints, but they are difficult to measure consistently (see Sarjeant 1975) and are often so variable that they are of questionable value (see comments of Welles 1971). We have not attempted to compile detailed measurements of interdigital angles, and they will be mentioned only as approximate averages.

Pace length (PL) — the distance between corresponding points in two successive footprints (left and right, or right and left; see Fig. 2C).

Stride length (SL) — the distance between corresponding points in two successive prints of a single foot (see Fig. 2C).

With measurements of two successive paces (PL^a and PL^b), and of the stride (SL) that they encompass, it is possible to calculate *pace angulation* (ANG) as follows:

$$\cos ANG = \frac{(PL^a)^2 + (PL^b)^2 - (SL)^2}{2 \times (PL^a) \times (PL^b)}$$

The more nearly pace angulation approaches to 180° the narrower is the trackway and the less obvious is the zig-zag arrangement of its footprints (see Fig. 2C).

The ratios *pace length / footprint length* (PL/FL) and *stride length / footprint length* (SL/FL) are often used in definitions of ichnotaxa (see, for example, Lull 1953, Haubold 1971) and are also provided here. These ratios tend to increase as a track-maker accelerates, and they can therefore give a useful indication of a track-maker's gait. In calculating these ratios FL was taken to be the mean for the two footprints defining each pace or stride.

To calculate means and other statistics it was usually necessary to reduce sample sizes (N) by excluding data from damaged or badly distorted footprints.

DESCRIPTIONS

At first glance the dinosaur trackways at Lark Quarry present a rather confusing picture (Pl. 4). However, it soon becomes apparent that the trackways can be sorted into several natural groups on the basis of size, orientation, preservation and footprint shape. Five such groupings may be recognized.

A. Remnants of a few trackways made by fairly large bipedal dinosaurs. These remnants comprise scattered footprints which are very poorly preserved and have no preferred orientation. The footprints appear to have been tridactyl, with rather short, thick and bluntly-rounded toes, and they are tentatively attributed to ornithopod dinosaurs. They seem to have been formed, then eroded and filled with water-laid sediment, well before the substrate was exposed to the air and the other footprints were formed at Lark Quarry. It was not possible to obtain any accurate measurements, and these remnants of old trackways will not be considered further.

B. A single trackway of a medium-size bipedal dinosaur (B in Fig. 3). This trackway extends across the southern part of Lark Quarry from WSW to ENE, and is attributed to an ornithopod dinosaur. The tridactyl footprints have relatively short, broad and well-rounded digits (see example *a* in Fig. 4) and are referred to the same ichnotaxon as the many small footprints in group *D* (below). However, this trackway is much larger than any of those in group *D*, and it was certainly formed at an earlier date: some of its footprints were deeply impressed in soft waterlogged mud and others (in lower-lying areas) were partly destroyed by scouring. This trackway seems to have been formed at about the time the substrate was draining free of surface water and was becoming exposed to the air.

C. A single trackway of an exceptionally large bipedal dinosaur (C in Fig. 3). This trackway extends across the northern part of Lark Quarry from NE to SW, and is attributed to a carnosaur — a large representative of the Theropoda. The footprints are very obvious basin-like structures (Pl. 5, Fig. B), and some of them show clear traces of three tapering or V-shaped digits (Fig. 4).

D. Numerous trackways of small to medium-sized bipedal dinosaurs; extending from SW to NE (Fig. 3, Pl. 4). The footprints are well preserved and each of them comprises three fairly short, thick and bluntly rounded digits. These trackways are attributed to ornithopod dinosaurs, and their footprints may be found superimposed upon those of the carnosaur (*C*, above) and upon those of coelurosaurs (*E*, below).

E. Numerous trackways of small (and sometimes very small) bipedal dinosaurs; extending from SW to NE (Fig. 3, Pl. 4). Each of these trackways comprises footprints with three fairly long, narrow and sharply-pointed digits. The trackways are attributed to coelurosaurs (small dinosaurs of the suborder Theropoda), and their footprints may be found superimposed upon those of the carnosaur (*C*) and upon those of the ornithopods (group *D*).

Footprints in the latter three groups are equally well preserved, and all of them seem to have been formed at about the same time. These footprints were formed after the muddy substrate had been exposed long enough to have attained a firm plastic consistency. From the evidence of superimposed footprints it is clear that the carnosaur traversed the Lark Quarry area before some, at least, of the ornithopods and coelurosaurs did so.

The trackways attributed to ornithopods (group *D*) and coelurosaurs (group *E*) extend in a single direction, and among them it is common to find trackways coinciding, intersecting at low angles, or weaving together inextricably (Pl. 4 and 14). Moreover in some places the trackways of small, and even medium-size, individuals quite simply disappear: apparently these smaller dinosaurs were so light that their feet failed to break through the firmer patches of surface sediment. These discontinuities are especially noticeable among the coelurosaur trackways (group *E*); the coelurosaur track-makers seem to have had relatively large feet (by comparison with the ornithopod track-makers), and their widely-spread and probably rather springy toes seem to have functioned as analogues of snow-shoes. Many of the track-makers, both ornithopods and coelurosaurs, seem to have been roughly similar in size (the majority having hip height estimated at less than 50 cm), and the footprints in any one trackway are not always consistent in their shape or spacing. This combination of factors makes it difficult to trace any single trackway, with confidence, for more than a few strides. Consequently our descriptions and analyses are based, in the main, on relatively short sections of trackways. For the ornithopod dinosaurs (group *D*) we examined 57 sections of trackways; on average each of these comprises 3 strides (a sequence of 5 footprints). The longest section of ornithopod trackway studied here comprises 17 strides (a sequence of 19 footprints). For the coelurosaurs (group *E*) we examined 34 sections of trackways; here the average number of strides per section of trackway is between 3 and 4 (between 5 and 6 footprints). The longest section of coelurosaur trackway studied here comprises 22 strides (a sequence of 24 footprints). The difference in sample size (57 ornithopod trackways as opposed to 34 coelurosaur trackways) does not indicate that ornithopods were more abundant than coelurosaurs. On the contrary, the ornithopod track-makers were probably outnumbered by the coelurosaur track-makers (see p. 443). The sample sizes differ for two reasons. First, the coelurosaur trackways are affected by so many discontinuities that it is difficult to find sequences of more than a few paces. Second, the coelurosaur footprints show much less variation in size and shape than do the ornithopod footprints: coincident or intersecting trackways of ornithopods could usually be separated through differences in footprint size or footprint shape, but coincident or intersecting trackways of coelurosaurs were usually inextricable.

The trackways of the carnosaur, the ornithopods and the coelurosaurs are described in turn. But before proceeding to these descriptions it will be useful to consider the circumstances under which the trackways were formed. It is important to determine these circumstances because some of them (e.g. the consistency of the substrate) have a direct bearing on footprint morphology, while others (e.g. the physical geography) are pertinent to the behaviour of the track-makers.

The Winton Formation is a series of continental sediments that reaches a thickness of more than 1000 feet in the area around Winton (Casey 1966). The sediments are mainly sandstones, siltstones and mudstones, though there are some intraformational conglomerates and coal seams. Fragments of fossil wood are common, but other well preserved fossils are rare; these include angiosperm leaves, conifers, freshwater bivalves, lungfish toothplates and fragmentary remains of sauropod dinosaurs (Senior, Mond and Harrison 1978, Coombs and Molnar 1981). The Winton Formation is mid-Cretaceous in age (probably uppermost Albian to Cenomanian), and the conditions under which its sediments accumulated were well summarized by Senior et al. (1978, p. 15): 'Terrestrial-fluviatile, paludal, lacustrine. Low relief, wide river flats, local development of short lived lakes and swamps.'

The sediments at and around Lark Quarry are of lacustrine and fluviatile origin. At the time the dinosaur trackways were formed the Lark Quarry site seems to have represented part of a major drainage channel; it was most probably part of a platform lying on point bar deposits, a sand-spit, that had built out into a lake which deepened to the SW (see Fig. 25A). The Lark Quarry bedding plane now dips NW at 4°, but it originally had a run-off to the SW — as is indicated by the orientation of drag marks and prod-marks produced by floating vegetation (Pl. 4). At times of flood the lake would have spread over a wide area (including all three footprint localities) to deposit sand followed by muddy sediments. In the intervening periods the lake would have receded to become little more than a remnant water-hole surrounded by newly-exposed mud. It was during such a period that the trackways seem to have been formed.

The mud began to compact under water, and before it was fully exposed a single dinosaur traversed the southern part of the future Lark Quarry site from WSW to ENE. In this trackway (*B*) some footprints were formed as the animal crossed slightly elevated and newly-exposed patches of very soft sediment; the other footprints were formed in lower-lying areas of mud which were still covered by water. These lower-lying footprints were subsequently scoured and eroded as the remaining surface water drained off to the SW. At the future site of Lark Quarry the recently-laid sand and overlying mud were penetrated by narrow, vertical and unbranched tubes that probably mark the escape of buried arthropods (Pl. 2, Fig. B). Traces of similar escape burrows may be found at the Seymour Quarry site, along with horizontal and oblique tubular structures that seem to represent plant rootlets of various sizes (Pl. 1, Figs. A, B). The presence of plant rootlets might indicate that the mud was exposed sufficiently long for terrestrial vegetation to take hold. After the mud had been exposed for some time it was traversed by a single carnosaur and by numerous ornithopods and coelurosaurs (trackway groups *C, D* and *E* above). The mud was exposed long enough to achieve a firm plastic consistency, but not long enough for desiccation cracks to appear. The period of exposure would certainly have been a matter of hours, if not of days or weeks. Evidently the mud was not waterlogged at the time it was traversed by the dinosaurs: none of the thousands of footprints collapsed or slumped after withdrawal of the track-maker's foot. Nor does the mud seem to have been very tenacious, for there are very few instances in which it adhered to a track-maker's foot. In one of these (footprint No. 8 in Fig. 4) the mud adhering to the underside of a single toe was drawn up into a longitudinal crest; in another (Pl. 8, Fig. C) mud adhered to one toe in the form of a 'cusp' or 'bubble-like' structure. However, we suspect that in many cases the imprints of one or more digits have been narrowed by suction created during withdrawal of the track-maker's foot. Overall it seems that the mud may have had the consistency of potter's clay at the time it was traversed by the dinosaurs.

CARNOSAUR TRACKWAY

Ichnogenus cf. *Tyrannosauropus* Haubold 1971

Eleven footprints at Lark Quarry are far bigger than any others, and form a single trackway extending from NE to SW (Figs 3 and 4, Pls 4 to 6). This trackway is attributed to a carnosaur — a large bipedal predator of the dinosaur suborder Theropoda (order Saurischia).

It was not feasible to collect any of the carnosaur footprints, for to do so it would have been necessary to destroy many other trackways. In any case, the footprints do not show sufficient detail to warrant their assignment to any new or existing ichnospecies. Measurements of the carnosaur trackway were taken directly from the bedding plane at Lark Quarry and were checked on fibreglass replicas (QM F10322) at the Queensland Museum.

DESCRIPTION.

The trackway comprises deep, basin-like and rather 'messy' footprints, often with poorly defined margins. Evidently the track-maker's feet plunged right through the muddy surface layer and churned up the underlying sandy sediment. In most cases the impact of the foot caused sediment to bulge up between the toes and behind the foot to leave a prominent raised rim to the footprint (Pl. 5, Fig. B). The sandy sediment in the floor of the footprint is usually raised into a series of irregular ripples. Two of the carnosaur footprints have been illustrated elsewhere (Thulborn and Wade 1979, fig. 2), and two more examples are shown here (Pls 5 and 6). The following description is a generalized one, based on information from all better-preserved footprints in the trackway.

Each footprint is tridactyl, with clear imprints of digits 2, 3 and 4, but with no trace of the hallux (digit 1). The three digits are relatively short, emerging from a large basin-like depression representing a 'sole' or 'pad' to the foot; in footprint No. 3, for example, the length of digit 3, as a free entity, represents only about 41% of total footprint length (Pl. 5, Fig. A). The digits are usually quite sharply defined, but often there is no clear outline to the back of the foot, making it difficult to obtain a measurement of total footprint length (see, for example, Pl. 5). All the better-preserved footprints are slightly narrower than long, with footprint width equivalent to some 85–90% of footprint length. The digits are broad and straight, and taper sharply to V-shaped tips. In none of the footprints are there traces of digital swellings or nodes that might indicate the phalangeal formula. Digits 2 and 4 are distinctly shorter than digit 3, and are roughly mirror-images — being almost complementary in shape, size and angle of divergence from digit 3. In one of the best-preserved footprints (No. 3; Pl. 5, Fig. A) the interdigital angles are about 33° (2–3) and 30° (3–4).

Mean measurements of footprint size, pace length and stride length are as follows (each with standard deviation and coefficient of variation):

Mean FL: 51.4 ± 6.5 cm (CV 13%; N 7)
Mean FW: 46.1 ± 4.0 cm (CV 9%; N 10)
Mean PL: 166.6 ± 26.5 cm (CV 16%; N 10)
Mean SL: 330.6 ± 37.4 cm (CV 11%; N 9)
Mean ratio FW/FL: 0.88 ± 0.05 (CV 6%; N 7).

The near-symmetrical footprints are arranged with slight positive rotation (i.e. they point not only forwards, but slightly inwards). They form a narrow trackway, with mean pace angulation calculated at 170°47' (SD 9°26'; CV 5.5% N 9). The trackway has a slightly sinuous course from NE to SW. From the spacing and orientation of the first few footprints we suspect that the animal actually approached the present Lark Quarry site from the NNE; the orientation of the last (11th) footprint indicates that the animal made an abrupt right-hand turn and moved off to the NW (see Fig. 3). There is no trace of a tail drag.

Some of the footprints show additional details of interest. Footprint No. 7, for example, consists of little more than shallow imprints of the three digits (Pl. 6), and seems to have been formed on a relatively resistant patch of sediment. In this footprint there is evidence that the tips of the digits extend forwards, beneath the surface of the sediment, as conical tunnels about 4 cm in length. These tunnels appear to be marks of long, robust and sharply-pointed claws. Traces of similar claws occur in several other footprints of the carnosaur. In footprint No. 8 the central digit (3) is unusually broad and contains a longitudinal crest of mudstone in the midline (Fig. 4; see also Thulborn and Wade 1979, fig. 1B). This crest was presumably formed by mud adhering to the underside of the middle toe as the animal's foot was lifted from the substrate; other prints from the same foot do not show this feature. Fig. 4 illustrates variation in shape of the carnosaur's footprints.

STATUS AND AFFINITIES.

The occurrence of a carnosaur trackway at Lark Quarry is not unduly surprising. Carnosaurs seem to have had an almost world-wide distribution during the Cretaceous period, with their footprints having been reported as far afield as Spitzbergen (Edwards et al. 1978) and Western Australia (Colbert and Merrilees 1968). No skeletal remains of carnosaurs are recorded from Queensland, though footprints of large theropod dinosaurs are well known in the Jurassic rocks of the state (Ball 1933, 1934a, 1934b, 1946; Anonymous 1951, 1952a, 1952b; Staines 1954; Bartholomai 1966). For the sake of convenience we may distinguish two major groupings of carnosaur footprints in general: those with relatively long and slender toes, and those with comparatively short and thick toes. Examples of these two groupings are, respectively, *Megalosauropus* and *Tyrannosauropus* (see Haubold 1971 and references cited therein). The former are probably footprints of smaller and more gracile carnosaurs, such as *Allosaurus* and *Megalosaurus*, while the latter probably represent bigger and more robust forms like *Tyrannosaurus*. The footprints of the Lark Quarry animal have rather short thick toes, and they appear to be closer in appearance to *Tyrannosauropus* than to any other form of carnosaur footprint so far described. The Lark Quarry footprints resemble *Tyrannosauropus* in general shape and proportions (mean ratio FW/FL of 0.88 as opposed to approximately 0.86 in *Tyrannosauropus*), but they differ in the following respects: in size (FL up to 80 cm in *Tyrannosauropus*), in pace angulation (170° as opposed to approximately 150°), and in the ratio SL/FL (6.4 as opposed to 5.0). On the basis of these similarities and differences we recommend that the Lark Quarry footprints should be referred to as cf *Tyrannosauropus*. This identification does not imply that the theropod dinosaur *Tyrannosaurus* was responsible for the Lark Quarry trackway; the track-maker can be identified no more precisely than 'carnosaur'.

It must be mentioned here that footprints of carnosaurs have often been confused with those of ornithopod dinosaurs (bipedal herbivores of the suborder Ornithopoda, order Ornithischia). The source of this confusion is partly historical: the first footprints to be attributed to a particular genus of dinosaur — the ornithopod *Iguanodon* — happened to be large tridactyl examples from the Lower Cretaceous of Europe. Subsequently, there grew a common tendency for *any* large tridactyl footprints to be ascribed to *Iguanodon* or to some similar ornithopod dinosaur (see comments by Beckles 1862, Charig and Newman 1962, Sarjeant 1974). Such confusion has, in fact, occurred over footprints from the Australian Cretaceous: large tridactyl prints from the Broome Sandstone (Lower Cretaceous) of Western Australia were attributed to iguanodonts by McWhae et al. (1958), but were later identified as those of theropod dinosaurs (Colbert and Merrilees 1968). Iguanodontids and some theropods both produced large tridactyl footprints which may, in some circumstances, be difficult to distinguish — particularly if preservation is poor. It has been suggested to us (by Dr D.B. Norman, pers. comm.) that some doubt may attach to the footprints of the Lark Quarry animal, and that these might actually be footprints of an iguanodontid ornithopod. However, several distinctive features of the footprints lead us to conclude that they are almost certainly those of a carnosaur. First, the footprints are slightly longer than broad, whereas those of ornithopods are commonly broader than long (see, for example, Langston 1960, Currie and Sarjeant 1979, and the many ornithopod footprints described below). Next, the three digits have an almost symmetrical arrangement; in many ornithopod footprints digit 2 is more widely spaced from digit 3 than is digit 4 (see same examples). Third, the Lark Quarry footprints have traces of a large pointed claw on each toe; the ungual phalanges of the larger ornithopods were blunter, and sometimes rather hoof-like, structures. Finally, the central digit (3) is V-shaped in outline; in ornithopod footprints digit 3 tends to have roughly parallel margins that curve round to form a U-shaped extremity. These basic distinctions seem to confirm that the large trackway at Lark Quarry is that of a carnosaur (see Fig. 4).

ORNITHOPOD TRACKWAYS

Ichnogenus *Wintonopus* ichnogen. nov.

Type and only ichnospecies *W. latomorum* ichnosp. nov.

HOLOTYPE: single right footprint, preserved as natural mould; QM F10319 (Pl. 7, Fig. A).

REFERRED MATERIAL: QM F10320 (single left footprint, as natural mould; Pl. 11, Fig. A); QM F10321 (rock slab with footprints and trackways as natural moulds); QM F12264 (single right footprint, as natural cast; Pl. 1, Figs. A, B); QM F10322 (fibreglass replicas of footprints and trackways preserved as natural moulds; Pl. 8 to 10; Pl. 11, Figs. B, C, D; Pl. 13, Fig. C; Pl. 14, Fig. A; Pl. 16, Figs. B, C).

LOCALITIES: Lark Quarry (QM F10319, QM F10320, QM F10321, QM F10322); Seymour Quarry (QM F12264). See Fig. 1 for location of quarries.

HORIZON: interbedded sandstones and mudstones about the middle of the Winton Formation; early Upper Cretaceous (Cenomanian).

ETYMOLOGY: Ichnogenus name derived from the name Winton and the Greek *pous* (foot); ichnospecies name (from Latin *latomus*, stone-mason) as tribute to the many volunteers who worked at the Lark Quarry excavation.

DIAGNOSIS (ichnogenus and ichnospecies): narrow trackway of small to medium-size digitigrade biped, with pace angulation about 160°. Footprint size index (SI) usually between 3.2 and 11.1 cm, but occasionally as high as 26.6 cm. No imprints of hand or tail. Footprints tridactyl (digits 2, 3 and 4), slightly broader than long (ratio FW/FL about 1.15), showing distinct positive rotation. Digits broad, with rounded or bluntly angular tips, without indications of phalangeal pads. Digit 3 longest, with sub-parallel sides. Digit 4 shorter and slightly narrower than digit 3, extended as blunt posterior salient. Digits 3 and 4 close together, parallel or only slightly divergent. Digit 2 shortest, and widely separated from digit 3 (with interdigital angle often about 60°). Imprints of digits 2 and 3 sometimes completely separated. Posterior margin of foot convex forwards. Ratio PL/FL usually between 8.0 and 13.5, rarely as low as 4.0 or as high as 15.0; ratio SL/FL usually between 16.0 and 24.0, rarely as low as 8.0 or as high as 27.0.

DESCRIPTION. The holotype is a sharply defined footprint, probably formed by the foot penetrating and leaving the substrate with minimal disturbance (Pl. 7, Fig. A). Few of the footprints referred to *Wintonopus latomorum* are identical to the holotype: the majority have less complete imprints of the digits, and many appear to have been disfigured by withdrawal of the track-maker's foot from the sediment. Nevertheless all these disfigured and less complete examples can be interpreted as variants of the footprint pattern exemplified by the holotype (see Fig. 5). Variation in shape of the footprints is described first; thereafter we describe variation in size, proportions and spacing of the footprints.

All the footprints are tridactyl. They are often several centimetres deep, yet none of them shows any trace of digit 1. If this digit was present in the track-maker's foot it must have been quite short and non-supportive, so that it failed to touch down even when the three weight-bearing digits sank quite deeply into the mud. Digit 1 was probably no longer than it is in ornithopods such as the Lower Cretaceous *Hypsilophodon* (Fig. 6B). The imprint of digit 4 extends farther back than the imprints of digits 2 and 3, giving the impression of a distinct salient or 'spur' at the posterolateral corner of the footprint. This 'spur' is unlikely to indicate the presence of a functional digit 5 (which is vestigial in even the earliest ornithopod dinosaurs) and probably reflects that the distal end of metatarsal 4 was located well to the rear of the foot, in standard ornithopod fashion (see, for example, the foot of *Fabrosaurus* — Thulborn 1972, fig. 12B).

Nearly all the footprints are asymmetrical, with a strongly divergent digit 2, so that isolated examples are readily identified as left or right. This method of identification has been verified in at least 60 *Wintonopus* trackways. Only a few footprints (in otherwise typical trackways) show any close approach to a symmetrical arrangement of the three digits. These near-symmetrical prints could have been produced in any of several ways: by some degree of spreading and/or closure of digits in the foot; by partial flexion of the divergent digit 2; by rotation of the foot around the long axis of digit 3 (so that digit 2 was carried laterally and slightly underneath digit 3); by the foot meeting the substrate at an unusual oblique angle (with the long axis of digit 3 directed forwards, downwards and slightly outwards).

The imprints of the digits are usually quite short and relatively broad. In most footprints the three digits are about equally broad (as, for example, in the holotype), but in a few cases digit 3 is much broader than digits 2 and 4 (e.g. Pl. 9, Fig. D; Pl. 10, Fig. D). In these examples digit 3 seems to have borne most of the track-maker's weight, while the flanking digits splayed out to form smaller and shallower imprints. A very similar effect was described by Sternberg (1932) in an ornithopod footprint (*Gypsichnites pacensis*) from the Lower Cretaceous of British Columbia. Digit 3 is longest, and in the least-disfigured footprints digits 2 and 4 extend about equally far forwards. The imprint of digit 3 is often straight, but sometimes shows very slight curvature (convex laterally; e.g. Pl. 11, Fig. A; Pl. 15, Fig. B). The hindmost margins of digits 2 and 3 lie on a line approximately normal to the long axis of digit 3, whereas digit 4 extends well behind this line to form the posterior salient or 'spur'. In consequence the posterior margin of the footprint (or the line connecting the hindmost points of the three digital imprints) is arched forwards. In some footprints, such as the holotype, the three digital imprints are joined together posteriorly, and the arched rear margin is continuous. Evidently these footprints were formed by the foot sinking into the mud up to, or beyond, the distal end of the metatarsus. In many other examples the foot did not sink so deeply, so that the three digital imprints are partly or completely separated and there is no continuous rear margin to the footprint (e.g. Figs 5D, E, F; Pl. 8, fig. B). The imprint of digit 2 is often completely separated from that of digit 3, whereas the imprints of digits 3 and 4 are usually joined together (e.g. Pl. 8, Figs A, B, D). This difference probably indicates that digit 2 diverged from digit 3 higher up the metatarsus than did digit 4 (see foot skeletons of ornithopods, Fig. 6). There are no certain indications of phalangeal pads in any of the footprints. The tips of the digital imprints are generally well-rounded in outline — except where they have been extended forwards as scrape-marks (see below) — but are sometimes a little sharper in the smallest footprints (Pl. 11). Interdigital webbing is limited in extent; the holotype shows traces of a small web between digits 3 and 4, and less certain traces of another between digits 2 and 3.

Wintonopus material from Seymour Quarry comprises natural casts reinforced by superficial infiltration of ironstone. The surfaces of the casts are wrinkled and finely tuberculate, and somewhat reminiscent of reptilian skin texture (Pl. 1). However, it is not certain that these specimens do show preservation of skin texture: an apparently identical texture is found on footprint casts attributed to the coelurosaurs and on some areas of seemingly undisturbed sediment, and it may be no more than a by-product of ironstone formation.

Practically every *Wintonopus* footprint at Lark Quarry seems to have been disfigured to some extent as the track-maker's foot was withdrawn from the mud. Basically, each foot sank quite deeply into the mud, and as it was lifted clear at the end of the stride the tips of one or more digits tended to drag and scrape through the rim of the newly-formed footprint. So, in many cases, there are scrape-marks extending forwards from one or more of the digital imprints. Digit 3 was longest in the foot and, for that reason, tended to produce a scrape-mark most frequently (e.g. Pl. 8, Fig. A). Digit 4 was intermediate in length between digits 2 and 3, and was next most likely to produce a scrape-mark, whereas digit 2 was shortest (parallel to the long axis of digit 3) and rarely did so (e.g. Pl. 10, Fig. D). In most cases the scrape-marks are fairly short, but in a few examples they are longer than the digital imprints (Pl. 8, Fig. A, and Pl. 10, Fig. D). The scrape-marks are not straightforward extensions of the digital imprints, but veer away from them at a distinct angle. Sections of trackways show that each foot was planted into the mud with slight positive rotation (i.e. with the toes pointing forwards and inwards). But as the foot was lifted from the mud it evidently turned to face directly ahead, so that the tips of the toes swept forwards and slightly outwards. In other words the foot was placed in the mud at one angle and was withdrawn at a different angle, and it is for this reason that the digital imprints have a different orientation from their scrape-marks. In some footprints this effect is so marked that the tip of digit 3 appears to be forked or Y-shaped (e.g. Pl. 8, Fig. D, and, to a lesser extent, in the holotype). In such examples the medial branch of the fork was formed when the digit was placed into the mud, and the lateral branch is a scrape-mark produced when the digit was withdrawn in a different direction. An exactly comparable type of scrape-mark was illustrated by Sarjeant (1970, Fig. 5e) in an ornithopod footprint (? *Satapliasaurus* cf. *S. dsocenidzei*) from the Middle Jurassic of Yorkshire, England.

Clear examples of backwardly-directed scrape-marks are less common. Again, the longest digit (3) seems to have produced a scrape-mark most frequently whereas the shortest digit (2) rarely produced one. These scrape-marks are also aligned at a slight angle to the long axes of the digital imprints (e.g. Pl. 8, Fig. B), confirming that the tips of the digits swung laterally as the foot was lifted from the substrate.

The development of these scrape-marks (whether forwards or backwards) is best understood in relation to the sequence of events during the track-maker's stride cycle (Fig. 7). At the start of this cycle the forwardly-extended foot would have been planted into the sediment with slight positive rotation (Stage 1 in Fig. 7). The initial footprint would have been quite shallow. At mid-stride the track-maker's centre of gravity would have passed forwards above the foot, which would then have sunk deeper into the substrate (Stage 2 in Fig. 7). In many instances the foot also slipped backwards a little, so that the front margins of the footprint are distinctly 'stepped' or 'terraced' (see, for example, Pl. 8, Figs. A, B; Pl. 9, Fig. D). Shortly thereafter the foot began to rotate (so that the long axis of digit 3 was directed straight ahead), and the rear part of the foot started to lift clear of the substrate. Sometimes the toes continued to slip backwards as they were lifted from the footprint: in these cases the toe-tips incised deep slots in the floor of the footprint (Stage 3A in Fig. 7) or even breached the rear wall of the footprint to leave backwardly-directed scrape-marks (Stage 3B). More commonly there was limited back-slip of the toes (Stages 1 to 2) and the toes-tips dragged through the front wall of the footprint to produce forwardly-directed scrape marks (Stage 3C).

Wintonopus footprints are typically broader than long, even though many examples have their total length exaggerated by scrape-marks. In some cases the track-maker's foot was planted into the mud at a steep angle, to leave relatively short and stubby imprints of the toes (e.g. Pl. 8, Fig. B). In other cases the foot seems to have lost its purchase in the muddy substrate, and the toes slithered back to form deep scratches that exaggerate the total length of the footprint (e.g. Pl. 9, Fig. B). In still other cases only the distal parts of the toes entered the mud, and then skidded backwards to produce a footprint consisting of little more than three long scratch-marks (e.g. Pl. 10, Fig. A). A few footprints consist of three puncture-marks apparently formed by the toes entering and leaving the mud almost vertically (e.g. Pl. 15, Fig. C).

Measurements of footprints, paces and strides were taken from parts of 57 different trackways of *Wintonopus* (see 'Methods' for descriptions of measurements). Fifty-six of these trackways are on the Lark Quarry bedding plane; the other section of trackway is at a different site — New Quarry. The 56 trackway sections at Lark Quarry comprise 284 footprints, representing 228 paces and 172 strides. This sample provides the following mean figures for dimensions of footprints, paces and strides:

Overall means

Mean FL: 6.71 ± 3.39 cm (CV 51%; N 200)
Mean FW: 7.58 ± 4.51 cm (CV 60%; N 214)
Mean PL: 68.3 ± 32.2 cm (CV 47%; N 215)
Mean SL: 131.7 ± 63.4 cm (CV 48%; N 162)

The high coefficients of variation reflect considerable ranges in size. Nearly all the trackways are those of small animals, with footprint lengths between 2 cm and 16 cm, and stride lengths in the range 49–271 cm; but the size distribution, as a whole, is attenuated by the presence of a single very large trackway with footprints up to 33 cm long and stride lengths reaching 345 cm (trackway 'B' in Fig. 3; see Figs 8 and 10).

The index of footprint size, the pace angulation and various ratios were calculated from the basic measurements listed above (see 'Methods'); they have the following means:

Overall means
Mean SI: 7.20 ± 3.93 (CV 55%; N 173)
Mean ANG: 161°24' ± 11°20' (CV 7% N 145)
Mean ratio FW/FL: 1.15 ± 0.25 (CV 22%; N 173)

*Mean ratio PL/FL: 10.18 ± 2.00 (CV 20%; N 120)
*Mean ratio SL/FL: 19.84 ± 3.69 (CV 19%; N 88)
(* FL is mean for two footprints defining each pace or stride)

Footprint proportions (FW/FL) and pace angulation appear to show relatively little variation, and are probably good diagnostic characters; that is, *Wintonopus* trackways are characterized by being narrow, and fairly straight, and by having footprints that are usually broader than long.

There is a strong positive correlation between any two measurements of size in the *Wintonopus* trackways and footprints; for example:

	product moment correlation coefficients	
variables	untransformed data	log transformed data
FL : FW (N 174)	0.87	0.89
*FL : PL (N 112)	0.86	0.87
*FL : SL (N 79)	0.87	0.89
*FW : SL (N 89)	0.89	0.93
*SI : SL (N 59)	0.90	0.92

(*mean for two footprints defining each pace or stride)

The correlations between stride length and footprint dimensions (FL, FW or SI) are worthy of note. It is only to be expected that bigger animals would take bigger strides, but stride length varies according to the gait and speed of an animal — and not simply to its size alone. The impressive correlations between foot size and stride length imply that the *Wintonopus* trackmakers at Lark Quarry were all using a similar gait; in a random sample of dinosaur trackways one might expect to find a somewhat looser correlation between stride length and footprint dimensions.

The correlation between footprint size (SI) and footprint proportions (ratio FW/FL) is much poorer: 0.22, with untransformed data, N 172. So, too, is that between footprint length and pace angulation (0.23, with untransformed data, N 73). These poor correlations seem to confirm our observation that footprint proportions and pace angulation tend to remain fairly constant throughout the entire size range of *Wintonopus* trackways (see further discussion below).

All the preceding estimates and statistics are based on pooled data from the *Wintonopus* trackways (i.e. on every available example of the 284 footprints and their paces and strides). If the data are grouped, and mean figures are taken for each of the 56 trackways studied, there emerges a somewhat similar pattern of size distribution and correlations (see Figs 9 and 10). Means based on the grouped data may be summarized as follows:

Means per trackway
Mean FL: 6.64 ± 3.07 cm (CV 46%; N 56)
Mean FW: 7.55 ± 4.36 cm (CV 58%; N 56)
Mean PL: 67.1 ± 30.6 cm (CV 46%; N 55)
Mean SL: 128.0 ± 59.6 cm (CV 47%; N 52)
Mean SI: 7.05 ± 3.58 cm (CV 51%; N 56)
Mean ANG: 162°47' ± 8°46' (CV 5%; N 51)
Mean ratio FW/FL: 1.14 ± 0.19 (CV 18%; N 56)
Mean ratio PL/FL: 10.18 ± 1.97 (CV 19%; N 49)
Mean ratio SL/FL: 19.75 ± 3.50 (CV 18%; N 44)

Most coefficients of variation remain very high. An analysis of variance (see Sokal and Rohlf 1969, p. 204 *et seq.*) will reveal how much of this variation lies within the *Wintonopus* trackways:

variable	*variation within trackways* (%)	*variation among trackways* (%)
FL	15.1	84.9
FW	6.0	94.0
PL	7.5	92.5
SL	2.4	97.6
SI	0.8	99.2
ratio FW/FL	52.1	47.9
ANG	77.9	22.1

Evidently footprint dimensions, pace length and stride length remain fairly constant within the *Wintonopus* trackways. Footprint length is somewhat more variable than footprint width within the trackways, but the index of footprint size is virtually constant. (Footprint length is more variable than footprint width because it is more strongly affected by the angle at which the foot enters and leaves the substrate, and by the development of scrape-marks; see Fig. 5). Stride length appears to be remarkably consistent within trackways, though pace length is more variable. Footprint proportions (ratio FW/FL) and pace angulation appear to vary more within trackways than they do between trackways; but these two features show little overall variation in the first place — so they may still be regarded as good diagnostic characters. In general, most of the variation in footprint dimensions, paces and strides can be attributed to the difference in size between one trackway and another.

STATUS AND AFFINITIES. The footprints referred to *Wintonopus latomorum* vary a good deal in size and in appearance, yet they all show some at least of the following diagnostic characters: a widely spaced or divergent digit 2, a backwardly-projecting 'spur' behind digit 4, a forwardly-arched rear margin, and a width that equals or exceeds footprint length. Where the footprints can be connected into trackways they are arranged with distinct positive rotation, and the trackways are always narrow and rather straight (with pace angulation about 160°). Moreover, footprint dimensions are strongly correlated one with another, and with stride length. In short, all the footprints may be regarded as those of animals sharing one distinctive pattern of foot structure (see Fig. 6C) and using the same gait. For these reasons it seems justifiable to assemble all these footprints in a single ichnospecies. Differences in shape between one footprint and another appear to be no more than circumstantial (see preceding descriptions and Fig. 5). According to recent recommendations for the nomenclature of trace fossils (see Article 40 in Basan 1979) it might be legitimate to define several ichnospecies of *Wintonopus* on the basis of footprint shape alone — e.g. a 'scratchy-toed' species, a 'stubby-toed' species, and so on. In the present circumstances, where footprint shape varies within a single trackway, such a measure would be rather confusing. Moreover there is no clear evidence that *Wintonopus* footprints of different morphology were 'produced in different phases of behavior' on the part of the track-maker (as Basan's Article 40 seems to require). In addition it may be noted that the range of variation in *Wintonopus* is no greater than that in some existing ichnotaxa — e.g. the ichnogenus *Anomoepus* (as defined by Lull 1953), and the ichnospecies *Grallator variabilis* and *G. olonensis* (as defined by de Lapparent and Montenat 1967).

The makers of the *Wintonopus* trackways were almost certainly dinosaurs of the suborder Ornithopoda (bipedal herbivores of the order Ornithischia). Ornithopods had a world-wide distribution during the Mesozoic era: their skeletal remains and their footprints have been reported from every continent except Antarctica. The following features of *Wintonopus latomorum* seem to be characteristic of very many ornithopod footprints: the footprint is tridactyl, and its width rivals or exceeds its length; the digital imprints are relatively short, thick and blunt (indicating the presence of 'hoof-like' unguals rather than sharp claws); the space between digits 2 and 3 is distinctly greater than that between digits 3 and 4; the outer margins of digits 2 and 4 diverge only slightly from the longitudinal axis of digit 3, so that the footprint has sub-parallel sides; there are sometimes traces of small interdigital webs. In all these features *W. latomorum* resembles other footprints attributed to ornithopod dinosaurs — e.g. *Amblydactylus* ichnospp. from the Lower Cretaceous of Canada (Sternberg 1932, Currie and Sarjeant 1979); unnamed types from the Late Jurassic/Early Cretaceous of Mexico (Ferrusquia-Villafranca et al. 1979); footprints of *Iguanodon,* from the Lower Cretaceous of Europe (Beckles 1862, Dollo 1906). However, the footprints described here are distinctly smaller than many others attributed to ornithopod dinosaurs (see Table 1). Of the 57 *Wintonopus* trackways examined in this study only two have mean SI greater than 12 cm (actually 12.7 cm and 26.6 cm); among other footprints attributed to ornithopods only those of *Anomoepus* ichnospp. are commonly found to be so small. Aside from this *Wintonopus* differs from most other ornithopod footprints in one other respect — in the absence (or weak development) of an imprint representing a 'sole' or 'heel' to the foot. The rear margin of the footprint is concave (arched forwards) rather than convex (arched backwards) and presumably corresponds to the natural arch formed by the distal ends of the metatarsals. This distinctive footprint shape seems to indicate that the *Wintonopus* track-makers were thoroughly digitigrade, whether they were walking or running (see later discussion of speeds and gaits). These differences in size and shape are sufficient to distinguish *Wintonopus* from most other tracks attributed to ornithopod dinosaurs. *Anomoepus* ichnospp. are comparable in size to *Wintonopus,* but are distinguished by narrower and more acutely pointed digits with obvious phalangeal nodes (see Lull 1953). In addition most examples of *Anomoepus* have the ratio PL/FL much lower than it is in *Wintonopus* (Fig. 11).

However, two types of footprint described by de Lapparent and Montenat (1967) from the Rhaeto-Liassic of Vendée (W France) bear some definite resemblances to *Wintonopus.* One of these types, *Anatopus palmatus,* was also attributed to an ornithopod dinosaur but is, unfortunately, represented by only three isolated footprints. In all three cases footprint size index is about 9.0 cm — well within the range described for *Wintonopus;* the ratio FW/FL is about 1.14 — practically identical to the mean for *Wintonopus* (1.15). *Anatopus* appears to resemble *Wintonopus* not only in size, shape and arrangement of the three digits, but also in possessing what seem to be anterolaterally directed scrape-marks at the tips of digits 3 and 4 (see de Lapparent and Montenat 1967, fig. 16, but note the different identification of digits). Nevertheless *Anatopus* certainly differs from *Wintonopus* in that the digits are relatively narrow and show distinct outlines of phalangeal pads. Moreover, de Lapparent and Montenat identified traces of very extensive interdigital webbing in the type specimen of *Anatopus.* A second type of footprint, *Saltopoides igalensis,* was attributed to a theropod dinosaur but is, once again, rather similar to *Wintonopus* (see de Lapparent and Montenat 1967, Fig. 15). *Saltopoides* has a footprint size index about 13.4 cm, but the footprints differ from those of *Wintonopus* in being distinctly longer than wide (FW/FL ratio about 0.75). In addition the lateral and medial margins of the footprints are divergent (rather than parallel as in *Wintonopus*), and there is no very marked positive rotation of the footprints. *Saltopoides* also differs in showing faint indications of phalangeal pads, but in two other respects it is very like *Wintonopus* — in having high values for pace angulation (almost 180°) and for the ratio PL/FL (11.1). In summary, *Wintonopus* is similar to both *Anatopus* and *Saltopoides* in some features, but in neither case is there an exact correspondence in footprint morphology.

TABLE 1: A Comparison of Size Among Footprints Attributed to Ornithopod Dinosaurs.

mean index of footprint size (cm)		
68.5	'Ornithopoda', Jurassic of Brazil (Leonardi 1980)	
61.4	*Amblydactylus gethingi*, L Cretaceous of Canada (Sternberg (1932)	
51.3	*Iguanodon*, L Cretaceous of Portugal (Antunes 1976)	
46.3	*Irenesauripus acutus*, L Cretaceous of Canada (Sternberg 1932)	
28.6	*Gypsichnites pacensis*, L Cretaceous of Canada (Sternberg 1932)	
24.7	'Ornithopod morphotypes', Jurassic/Cretaceous of Mexico (Ferrusquia-Villafranca *et al.* 1978)	
23.5	*Satapliasaurus* cf *S. dsocenidzei*, M Jurassic of England (Sarjeant 1970)	
18.5	*Satapliasaurus dsocenidzei*, L Cretaceous of Georgia, USSR (Gabouniya 1951)	
18.3	*Amblydactylus kortmeyeri*, L Cretaceous of Canada (Currie and Sarjeant 1979)	
17.6	*Iguanodon*, U Jurassic of England (Delair and Brown 1974)	
17.5	?cf *Satapliasaurus*, M Jurassic of England (Sarjeant 1970)	
15.7	*Irenichnites gracilis*, L Cretaceous of Canada (Sternberg 1932)	
15.6	*Sauropus barrattii*	Triassic of Connecticut (Lull 1953)
15.0	*Anomoepus crassus*	
10.7	*Anomoepus isodactylus*	
9.2	*Anomoepus intermedius*	
9.0	*Anatopus palmatus*, Rhaeto-Liassic of France (de Lapparent and Montenat 1967)	
8.7	*Anomoepus curvatus*, Triassic of Connecticut (Lull 1953)	
7.7	*Anomoepus scambus*, Triassic of Connecticut (Lull 1953)	
7.2	*Wintonopus latomorum*	
6.2	*Anomoepus gracillimus*, Triassic of Connecticut (Lull 1953)	
5.4	*Anomoepus minimus*, Triassic of Connecticut (Lull 1953)	

COELUROSAUR TRACKWAYS

Ichnogenus *Skartopus* ichnogen. nov.

Type and only ichnospecies *S. australis* ichnosp. nov.

HOLOTYPE: single left footprint, preserved as natural mould; QM F10330 (Pl. 7, Figs. B, C).
REFERRED MATERIAL: QM F10321 (rock slab with footprints and trackways as natural moulds); QM F12265 (single right footprint, as natural cast; Pl. 1, Figs. C, D); QM F10322 (fibreglass replicas of footprints and trackways preserved as natural moulds; Pl. 10, Figs B, D; Pl. 12; Pl. 13, Figs A, B; Pl. 14; Pl. 15, Fig. A; Pl. 16).
LOCALITIES: Lark Quarry (QM F10330, QM F10321, QM F10322); Seymour Quarry (QM F12265). See Fig. 1 for location of quarries.
HORIZON: interbedded sandstones and mudstones about the middle of the Winton Formation; early Upper Cretaceous (Cenomanian).
ETYMOLOGY: Ichnogenus name derived from Greek *skartes* (nimble) and *pous* (foot); ichnospecies name refers to southern (Australian) provenance.
DIAGNOSIS (ichnogenus and ichnospecies): trackway of small digitigrade biped, with pace angulation about 150°. Footprint size index (SI) between 2.9 and 5.7 cm. No imprints of hand or tail. Footprints tridactyl (digits 2, 3 and 4), slightly longer than broad (ratio FW/FL about 0.95) showing distinct positive rotation. Digit imprints narrow, straight and sharply pointed, without indications of phalangeal pads. Digit 3 longest; digits 2 and 4 about equal in length, and almost equally divergent from digit 3 (both interdigital angles between 25° and 30°). Imprint of digit 4 extends slightly farther back than imprint of digit 2, but does not form a posterior salient or 'spur'. Traces of small interdigital webs sometimes present. Posterior margin of footprint is an oblique line (posterolateral to anteromedial), either straight or arched forwards. In some examples there is an imprint of the metapodium: this is sub-rectangular in outline and roughly equivalent in length to digit 3. Ratio PL/FL usually between 5.5 and 8.5, rarely as low as 5.2 or as high as 9.1; ratio SL/FL usually between 11.0 and 16.0, rarely as low as 10.6 or as high as 17.3.

DESCRIPTION: The holotype is a well-defined footprint, impressed in the substrate with minimal disturbance. In general the footprints identified as *Skartopus* show much less variation in shape than do those referred to *Wintonopus*. Once again, however, all the variations that do exist may be interpreted as circumstantial modifications of the footprint pattern shown by the holotype. Variation in footprint shape is described first; thereafter we describe variation in size, proportions and spacing of the footprints.

All footprints referred to *Skartopus* are tridactyl, with clear traces of digits 2, 3 and 4. The footprints sometimes reach a depth of 2 cm, or more, but none of them shows any certain trace of the hallux (digit 1). If the hallux was present in the track-maker's foot it must have been relatively short and without a major supportive role; presumably it extended no farther than the line of the metatarso-phalangeal contacts in digits 2, 3 and 4 (see Figs 6D–F). Where the three digits are deeply impressed, as in the holotype, it may be seen that their rear ends do not fall on a straight line. Digits 2 and 4 extend slightly farther back than digit 3, to form a curve (convex forwards) that presumably reflects the natural arch formed by the distal ends of the metatarsals.

Skartopus footprints are almost bilaterally symmetrical. It is sometimes difficult to identify isolated examples as left or right, but the following features are often useful guides: the space between digits 2 and 3 is slightly greater than that between 3 and 4; digit 2 is slightly more divergent than digit 4; scratch-marks, often present at the tips of the digit imprints, extends forwards and laterally. All these features are well shown in the holotype (Pl. 7, Figs B, C). Where the footprints can be connected into sections of trackway they are easily identified as left and right on account of their positive rotation (see Pl. 14, Fig. B).

The imprints of the digits are straight, and relatively long and narrow (by comparison with those of *Wintonopus*). In all cases the three digit imprints are about equally broad. Digits 2 and 4 are roughly equal in length, and digit 3 is longer. In nearly all examples the tips of the digit imprints are quite sharply pointed. The interdigital angles are small, and in some footprints digits 3 and 4 are sub-parallel (e.g. the holotype). There are no definite indications of phalangeal pads in any of the footprints. The holotype shows traces of small interdigital webs, as do several other footprints in the referred material (e.g. Pl. 12, Fig. D). *Skartopus* material from Seymour Quarry comprises natural casts with a finely wrinkled ironstone surface; it is not certain if this wrinkling is a representation of original skin texture (see Pl. 1 and p. 422).

Variation in footprint shape is less marked in *Skartopus* than in *Wintonopus.* Divarication of the digits is slightly more pronounced in some footprints than in others, but in all cases the digits form a near-symmetrical pattern. In most *Skartopus* footprints the digits terminate in sharp scratch-marks; apparently similar marks have been illustrated (though not described as such) in coelurosaur footprints from the mid-Cretaceous of Israel (Avnimelech 1966, pl. 7, fig. 2). Variation in the shape of *Skartopus* footprints is most easily explained by reference to events during the track-maker's stride cycle (Fig. 12). At the start of this cycle the forwardly-extended foot would have been planted on the sediment, and there would have been a very shallow initial footprint, or no footprint at all (Stage 1 in Fig. 12). At mid-stride the track-maker's centre of gravity passed forwards above the foot, which in *some* cases sank into the substrate (Stage 2A in Fig. 12). Later, as the rear part of the foot started to lift clear of the sediment, the claws pressed down and slightly backwards to produce sharp outlines to the tips of the digital imprints (Stage 3A in Fig. 12). At this point the toes sometimes started to slip backwards, their claws incising grooves in the floor of the footprint (Stage 4A in Fig. 12). This sequence of events produced sharp-toed tridactyl footprints such as the holotype (Pl. 7, Figs. B, C), some of which are secondarily deepened by backwardly-directed scratch-marks (e.g. Pl. 12, Figs. C, D; Pl. 13, Fig. A). However, in many other cases the foot did *not* sink into the substrate at mid-stride (Stage 2B in Fig. 12). To judge from the number of discontinuities (or 'missing' footprints) in *Skartopus* trackways this seems to have been a very frequent occurrence. There are at least two obvious reasons why the feet of *Skartopus* track-makers did not always leave recognizable footprints. First, the track-makers seem to have been remarkably small, and presumably light, dinosaurs (see Fig. 15). Second, it appears that coelurosaurs have bigger feet (relative to hip height) than many other bipedal dinosaurs (see later discussion concerning sizes of track-makers). It seems, then, as if the *Skartopus* track-makers may have been lightweight dinosaurs with large spreading feet that acted as analogues of snow-shoes. Even if the entire foot did not sink into the substrate the tips of the toes sometimes left imprints as the track-maker 'kicked off' at the end of its stride (Stage 3B in Fig. 12). The toes then slithered back through the mud to leave a series of curved parallel scratches (Stages 4B and 5B in Fig. 12). In some cases only one or two of the toes left such traces (e.g. Pl. 16, Fig. A).

A few *Skartopus* footprints are noteworthy in that they appear to include an imprint of the metapodium (e.g. Pl. 12, Figs A, B; Pl. 13, Fig. B). In these examples the imprint of the metapodium is a large sub-rectangular depression behind the three digit imprints. The metapodium imprint is no wider than the maximum spread of the digits, and it is roughly as long as the imprint of digit 3; it is widest at the rear, where it is broadly rounded in outline (convex backwards). Footprints with such traces of the metapodium are uncommon, and most of them occur singly and at random in the *Skartopus* trackways. However, one short section of trackway (a sequence of 3 paces) is composed entirely of such footprints (Pl. 14, Fig. B).

Measurements of footprints, paces and strides were taken from parts of 34 trackways of *Skartopus australis* (see 'Methods' for description of the measurements). All 34 trackways are on the Lark Quarry bedding plane, and they comprise a total of 191 footprints (representing 157 paces and 123 strides). This sample provides the following mean figures for measurements of footprints, paces and strides:

Overall means
Mean FL: 4.46 ± 0.70 cm (CV 16%; N 131)
Mean FW: 4.10 ± 0.56 cm (CV 14%; N 158)
Mean PL: 32.1 ± 4.0 cm (CV 12%; N 151)
Mean SL: 61.7 ± 7.8 cm (CV 13%; N 122)

The coefficients of variation are considerably lower than those for equivalent measurements in *Wintonopus* — in consequence of the much smaller size range in *Skartopus.* The index of footprint size, the pace angulation, and standard ratios were calculated from the basic measurements listed above (see 'Methods'); they have the following means:

Overall means
Mean SI: 4.29 ± 0.52 cm (CV 12%; N 126)
Mean ANG: 152°38' ± 11°44' (CV 8%; N 112)
Mean ratio FW/FL: 0.94 ± 0.16 (CV 17%; N 126)
*Mean ratio PL/FL: 7.27 ± 1.33 (CV 18%; N 97)
*Mean ratio SL/FL: 14.03 ± 2.26 (CV 16%; N 85)
(* FL is mean for two footprints defining each pace or stride)

Pace angulation appears to show relatively little variation, and is probably a good diagnostic character. In general terms pace angulation is about 10° greater in *Wintonopus* than in *Skartopus* — so that trackways of the latter tend to be slightly broader and to have a more obvious zig-zag arrangement of the footprints. In addition the footprints of *Skartopus* are commonly longer than broad whereas the reverse is true in *Wintonopus*.

There is generally a poor correlation between any two measurements of size in the *Skartopus* material; for example:

	product moment correlation coefficients	
variables	untransformed data	log transformed data
FL : FW (N 131)	0.36	0.34
*FL : PL (N 70)	0.04	0.16
*FL : SL (N 64)	0.07	0.07
*FW : SL (N 88)	0.23	0.20
*SI : SL (N 57)	0.15	0.10

(*mean for two footprints defining each pace or stride)

The correlations are not improved by transformation of the data. These poor correlations may be attributed, once again, to the limited size range of the footprints and trackways (see further discussion below). The correlation between footprint size index (SI) and footprint proportions (ratio FW/FL) is also poor (-0.19, with untransformed data; N 126), as is that between footprint length and pace angulation (-0.18, with untransformed data; N 61). The significance of these poor correlations will be examined later (p. 430).

A somewhat similar pattern of size distribution and correlations emerges if the data are grouped and mean figures are taken for each of the 34 *Skartopus* trackways (see Figs 14 and 15). Means derived from the grouped data may be summarized as follows:

Means per trackway

Mean FL: 4.46 ± 0.50 cm (CV 11%; N 34)
Mean FW: 4.14 ± 0.49 cm (CV 12%; N 34)
Mean PL: 32.0 ± 2.6 cm (CV 8%; N 34)
Mean SL: 61.8 ± 4.8 cm (CV 8%; N 34)
Mean SI: 4.28 ± 0.43 cm (CV 10%;, N 34).
Mean ANG: 153°37' ± 9°35' (CV 6%; N 34)
Mean ratio FW/FL: 0.94 ± 0.12 (CV 13%; N 34)
Mean ratio PL/FL: 7.19 ± 1.08 (CV 15%; N 29)
Mean ratio SL/FL: 13.73 ± 1.73 (CV 13%; N 32)

Analysis of variance (below) reveals that there is as much, or more, variation within trackways as there is among trackways:

variable	*variation within trackways* (%)	*variation among trackways* (%)
FL	57.9	42.1
FW	46.2	53.8
PL	79.9	20.1
SL	50.6	49.4
SI	52.1	47.9
ratio FW/FL	74.5	25.5
ANG	49.9	50.1

However, all these characters show little overall variation in the first place (see coefficients of variation) — so that most, if not all, of them may still be regarded as of diagnostic value.

STATUS AND AFFINITIES. The footprints designated *Skartopus australis* do not vary a great deal in size or in shape. They consistently show the following distinctive features: a near-symmetrical arrangement of three long, relatively narrow and sharply pointed digits, a forwardly arched rear margin (except where there is an imprint of the metapodium), and a length that equals or exceeds footprint width. Where the footprints can be connected into trackways they are found to be disposed with distinct positive rotation; the trackways are moderately broad, with pace angulation about 150°. By comparison the trackways of *Wintonopus* appear to be narrower, with pace angulation about 160°. Variation in shape of the *Skartopus* footprints appears to be circumstantial — the occasional appearance, in otherwise normal trackways, of footprints represented only by scratches or of footprints including a trace of the metapodium. The scratch-like footprints were probably formed when the track-maker's foot slipped backwards across the surface of the muddy substrate (Stages 2B to 5B in Fig. 12); footprints with a trace of the metapodium were presumably formed when the track-maker inadvertently came down 'flat-footed', or perhaps when the foot sank deeply in the mud. (Note, however, that one short section of trackway consists entirely of footprints with traces of the metapodium (Pl. 14, Fig. B). This sequence of footprints could be fortuitous, or it could derive from any of several factors — e.g. a pathological condition of the track-maker, or an accumulation of mud on the animal's feet.)

There is limited variation in size of the *Skartopus* footprints, paces and strides. The biggest footprint is less than twice the size of the smallest (in terms of SI); by contrast the biggest example of *Wintonopus* is nearly 12 times the size of the smallest. The coefficients of variation indicate that dimensions of footprints, paces and strides vary much less in *Skartopus* than they do in *Wintonopus* — yet the correlation between any two of these dimensions is in most cases very much poorer in *Skartopus* (compare Figs 10 and 15). These poor correlations do not necessarily indicate that the *Skartopus* material is a heterogeneous assortment of footprints and trackways: rather, they reflect the very limited range in size. For comparative purposes the entire sample of *Skartopus* tracks might be regarded as equivalent to a small size class selected from the *Wintonopus* sample. A very similar relationship between two ichnotaxa has been well illustrated by de Lapparent and Montenat (1967, fig. 8). In other words the *Skartopus* footprints and trackways are all roughly similar in their dimensions, so that there is as much (or more) variation within a trackway as there is between one trackway and the others (see analysis of variance). In addition it must be noted that the *Skartopus* footprints and trackways are, on the whole, much smaller than the *Wintonopus* footprints and trackways — yet both have been measured within the same limits of error. Small measurement errors would be of negligible importance in the large *Wintonopus* tracks, but they would certainly tend to blur correlations in the absolutely smaller *Skartopus* tracks. Overall the *Skartopus* footprints are quite consistent in size, shape, and their spacing within trackways; for these reasons it seems justifiable to assemble them in a single ichnospecies. The range of variation seen in this assemblage is no greater than that in several other ichnospecies attributed to coelurosaurs (e.g. *Grallator olonensis* and *G. variabilis*, de Lapparent and Montenat 1967).

The *Skartopus* footprints were very probably made by coelurosaurs — small representatives of the dinosaur suborder Theropoda. Skeletal remains and footprints of theropods have been recorded from every continent except Antarctica; theropod body fossils have not yet been reported from Queensland, though their footprints are well known in the state (for references see p. 420). In their size and general appearance the *Skartopus* footprints are comparable with those attributed elsewhere to coelurosaurs (see review by Haubold, 1971). The examples listed in Table 2 will illustrate the basic agreement in size. All these examples (including *Skartopus*) share the following similarities: the imprints of digits 2, 3 and 4 are rather narrow and quite sharply pointed; the digits diverge (usually) at low angles, and often have a near-symmetrical arrangement. However, *Skartopus* differs from nearly all other trackways attributed to coelurosaurs in having exceptionally high values for the ratios PL/FL and SL/FL (Fig. 16). *Skartopus* is also distinctive in its footprint morphology. It differs from *Columbosauripus* ichnospp. in the lesser divarication of the digits; in addition the digital

TABLE 2: A COMPARISON OF SIZE AMONG FOOTPRINTS ATTRIBUTED TO SMALL THEROPOD DINOSAURS.

mean index of footprint size (cm)	
24.3	*Anchisauripus minusculus*, Triassic of Connecticut (Lull 1953)
14.1	*Grallator formosus*, Triassic of Connecticut (Lull 1953)
12.2	*Columbosauripus* (2 ichnospp.), Cretaceous of Canada and Algeria (both ichnospp. illustrated by Haubold 1971, *q.v.*)
10.2	*Coelurosaurichnus* (5 ichnospp.), Triassic of Europe (all ichnospp. illustrated by Haubold 1971, *q.v.*)
8.1	*Grallator* cf *G. variabilis*, Triassic of Algeria (Bassoullet 1971)
7.5	*Anchisauripus hitchcocki*, Triassic of Connecticut (Lull 1953)
5.8	*Otouphepus magnificus*, Triassic of Connecticut (Lull 1953)
4.3	*Skartopus australis*
3.8	*Plesiornis pilulatus*, Triassic of Connecticut (Lull 1953)
3.7	*Wildeichnus navesi*, Jurassic of Argentina (Casamiquela 1964)
3.4	*Grallator gracilis*, Triassic of Connecticut (Lull 1953)
2.5	*Stenonyx lateralis*, Triassic of Connecticut (Lull 1953)
0.4	*Coelurosaurichnus* ichnosp., Triassic of England (Wills and Sarjeant 1970)

imprints of *Columbosauripus* tend to be broader than those of *Skartopus,* and digit 4 is often considerably longer than digit 2 (see Haubold 1971, fig. 47). *Coelurosaurichnus* ichnospp. are distinguished from *Skartopus* by very distinct imprints of claws and phalangeal pads, by the common preponderance of digit 4 over digit 2, and (in many cases) by having digit 3 noticeably broader than the flanking digits. In a few instances, however, *Coelurosaurichnus* does resemble *Skartopus* in having the rear margin of the footprint arched to the front. Similarly *Grallator* ichnospp. differ from *Skartopus* in possessing well developed phalangeal pads, traces of acuminate claws and, very often, a pronounced 'spur' formed by the backwards extension of digit 4 (see Lull 1953). *Stenonyx* may be distinguished from *Skartopus* by the same features and, in some instances, by the presence of a hallux imprint. *Wildeichnus* appears to differ in possessing a prominent 'spur' behind digit 3 and in showing a clear imprint of the hallux. To summarize, *Skartopus* is similar in basic morphology to other coelurosaur footprints, but it may be distinguished from these through differences in divarication and relative lengths of the digits, through lacking imprints of phalangeal pads or of acuminate claws, through the absence of a posterior 'spur', through the absence of a hallux imprint, through the relative straightness of the digits, and through its high values for the ratios PL/FL and SL/FL.

DISCUSSION

SIZES AND SPEEDS OF TRACK-MAKERS

From studies of locomotion in living terrestrial vertebrates Alexander (1976) determined the following relationship between stride length (λ, in metres), height at the hip (*h,* also in metres) and speed (*u,* in metres per second):

(*1*) $$\lambda/h \cong 2.3\,(u^2/gh)^{0.3}$$

In this equation λ represents our measurement for stride length (SL), and *g* is a constant — the acceleration of free fall; the ratio λ/*h* is termed 'relative stride length' (Alexander 1976). Alexander indicated that this relationship seems to hold true, at least in general terms, for large and small animals, both bipeds and quadrupeds, at gaits from slow walk to fast run. In addition he observed that the relationship does not seem to be seriously affected by variation in the consistency of the substrate. With additional data from fast-moving African ungulates Alexander, Langman and Jayes (1977) refined expression (*1*) to give:

(*2*) $$\lambda/h \cong 1.8(u^2/gh)^{0.39}$$

These authors concluded that expression (*2*) is best applied to animals that are cantering or galloping, whereas expression (*1*) is appropriate for animals using slower gaits. In mammals the change from a walking gait to a trotting gait occurs when λ/*h* is approximately 2.0 (Alexander 1976); the change from trotting to galloping follows when λ/*h* has increased to about 2.9. This latter figure is derived from two generalizations presented by Alexander (1977). The first of these is that mammals tend to shift from a trotting or racking gait to a galloping or cantering gait when the quantity $\hat{u}$ reaches a value of about 1.5. The quantity $\hat{u}$, or 'dimensionless speed', was defined by Alexander as follows:

(*3*) $$\hat{u} = u(gh)^{-0.5}$$

where *h* is expressed in metres and *u* is in m/s. The second generalization, which seems to apply to a wide variety of animals through a wide range of speeds, is that

(*4*) $$\lambda/h \cong 2.3\hat{u}^{0.6}$$

where λ/*h* represents mean relative stride length. From these generalizations it may be assumed that the shift from trotting to galloping occurs when

(*5*) $$\lambda/h \cong 2.3\,(1.5)^{0.6}$$
$$\lambda/h \cong 2.9$$

Consequently it is possible to identify the gaits of dinosaurian track-makers on the basis of relative stride length, as follows:

walk: $\lambda/h < 2.0$; locomotor performance equivalent to walking in mammals.
trot: $\lambda/h = 2.0$ to 2.9; locomotor performance equivalent to trotting or racking in mammals.
run: $\lambda/h > 2.9$; locomotor performance equivalent to cantering, galloping or sprinting in mammals.

To estimate the speeds of certain dinosaurs Alexander (1976) transformed expression (*1*) to give:

(*6*) $$u \cong 0.25g^{0.5}\lambda^{1.67}h^{-1.17}$$

This equation was then applied to data from dinosaur trackways, where λ could be measured directly (Alexander's λ = SL of our descriptions) and where *h* might be estimated from the size of the footprints. This method has since been applied to more than 50 dinosaur trackways, including a sample of those at Lark Quarry (Russell and Béland 1976; Tucker and Burchette 1977; Coombs 1978; Thulborn and Wade 1979;

Farlow 1981; Kool 1981; Thulborn 1981, 1982). Table 3 presents a summary of the speeds so far estimated in this way.

Figures listed in Table 3 for the Lark Quarry dinosaurs are preliminary estimates, and they will be revised in the present work. Our discussion will focus on the problem of estimating *h* on the basis of footprint dimensions. It is desirable that *h* should be estimated with reasonable care, because an underestimate will generate an overestimate of the track-maker's speed; conversely an overestimate of *h* will generate an underestimate of speed. In some instances the hindlimb length of a dinosaurian track-maker has been estimated from the evidence of pace length or stride length (e.g. Avnimelech 1966); an estimate of this type is of questionable value, simply because pace length and stride length vary according to the gait and speed of the track-maker (Lull 1953, p. 146). In other cases hindlimb length has been estimated on the basis of footprint dimensions; for example, Avnimelech (1966, p. 5) suggested that in the footprints of bipedal dinosaurs the length of digit 3 represented about 18% of hindlimb length. Elsewhere Alexander suggested (1976) that *h* could be calculated as approximately four times footprint length for a variety of dinosaurian track-makers, both bipeds and quadrupeds, and this suggestion has been rather widely accepted (see all sources cited in Table 3). However, Coombs (1978) expressed some reservations about this generalization, and Alexander (1976) did mention that footprint length could represent anything between 0.23*h* and 0.28*h* in the bipedal dinosaurs that he examined. In discussing the sizes and speeds of the Lark Quarry track-makers we will investigate some other methods for estimating *h*.

In comparing the sizes, weights and speeds of various dinosaurs Coombs (1978, Table 2) drew a

TABLE 3: SUMMARY OF SIZES AND SPEEDS PREVIOUSLY ESTIMATED FOR DINOSAURIAN TRACK-MAKERS.

ichnotaxa or track-makers	(N)	h (m)	u (m/s)	u (km/h)	λ/h	gait	source
Bipedal dinosaurs	(6)	0.6–2.1	1.2–3.6	4.3–13.0	1.2–2.5	walk (4) trot (2)	Alexander 1976
Sauropods	(2)	1.5–3.0	1.0–1.1	3.6–4.0	0.8–1.1	walk	
Ornithomimid	(1)	1.2	1.8	6.4	1.5^{e}	walk	Russell and Béland 1976
[a]Giant ornithopod	(1)	3.4	7.5	27.1	2.7^{e}	trot	
[a]Giant ornithopod	(1)	3.4	2.4	8.5	1.3	walk	Thulborn 1981
?*Anchisauripus*	(2)	$0.4–0.6^{e}$	$1.3–2.2^{x}$	4.5–7.9	$1.3–1.4^{e}$	walk	Tucker and Burchette 1977
Carnosaur	(1)	2.6	2.3	8.2	1.4	walk	Thulborn and Wade 1979 (Lark Quarry)
Ornithopods	(10)	<1.0	4.3^{m}	15.5^{m}	>2.0	trot/run	
Coelurosaurs	(10)	<1.0	3.6^{m}	13.0^{m}	>2.0		
Gypsichnites pacensis	(1)	1.2	2.0	7.2^{x}	1.8	walk	Kool 1981
Irenesauripus spp.	(3)	1.5–2.1	1.4–2.7	$5.0–9.7^{x}$	1.2–1.6	walk	
Irenichnites gracilis	(1)	0.6	2.8	10.1^{x}	2.3	trot	
Amblydactylus kortmeyeri	(1)	0.5	1.1	4.0	1.5	walk	
Tetrapodosaurus borealis	(1)	1.4	0.9	3.2^{x}	0.9	walk	
[f]Theropods	(3)	$1.2–1.5^{e}$	8.3–11.9	29.9–42.8	3.7–4.9	run	Farlow 1981
[s]Theropods	(3)	$1.5–1.8^{e}$	1.8–2.5	6.4–8.9	1.5–1.8	walk	
Theropods	(15)	1.5^{me}	4.2^{m}	15.2^{m}	2.3^{m}	trot	

a: two interpretations of single trackway.

f: three fastest of Farlow's 15 track-makers.

s: three slowest of Farlow's 15 track-makers.

e: figures estimated from published data.

m: mean.

x: Coombs (1978) provides different speed estimates, apparently through computational error (Farlow 1981).

distinction between ‘height at hips’ (as had been estimated by Colbert 1962) and ‘standard [or skeletal] hindlimb length’ (the sum of the lengths of femur, tibia and metatarsal 3). He indicated that there was sometimes a considerable difference between these two dimensions — particularly among large dinosaurs. In addition a rather similar distinction has been made between skeletal hindlimb length (*h*) and ‘height of the hindlimb’ (H) — the latter being defined as ‘the combined lengths of femur, tibia and longest metatarsal, plus an increment of 9% to account for ankle bones and for soft tissues at knee, ankle and sole’ (Thulborn, 1982, p. 228). For present purposes these various dimensions are assumed to be roughly equivalent, on the grounds that they are likely to be of great significance only in large dinosaurs. Our estimates of *h* for the Lark Quarry track-makers (Tables 4 and 5) are based on osteometric data and may be regarded as

TABLE 4: ESTIMATES OF SIZE, SPEED AND RELATIVE STRIDE LENGTH FOR 57 *WINTONOPUS* TRACK-MAKERS.

	estimated h	estimated speed		
	(cm)	(m/s)	(km/h)	estimated λ/h
1.	13.7	2.8–3.5 (3.1)	10.0–12.5 (11.2)	3.6–4.2 (3.9)
2.	16.8	3.3–4.0 (3.6)	11.9–14.3 (12.9)	3.8–4.3 (4.0)
3.	16.3	(3.5)	(12.6)	(4.0)
4.	16.8	3.0–3.3 (3.1)	10.6–11.8 (11.3)	3.5–3.8 (3.6)
5.	18.9	2.9–3.3 (3.1)	10.5–11.9 (11.2)	3.3–3.6 (3.4)
6.	18.6	(3.2)	(11.6)	(3.5)
7.	18.4	3.4–3.9 (3.7)	12.1–14.0 (13.5)	3.7–4.1 (4.0)
8.	19.7	3.0–3.1 (3.0)	10.6–11.3 (11.0)	3.3–3.4 (3.3)
9.	20.1	3.8–4.4 (4.1)	13.7–15.8 (14.7)	3.9–4.4 (4.2)
10.	18.4	3.1–3.8 (3.4)	11.2–13.8 (12.4)	3.5–4.1 (3.8)
11.	20.4	3.8–4.2 (4.0)	13.6–15.2 (14.4)	3.9–4.2 (4.1)
12.	23.7	2.6–3.2 (2.9)	9.4–11.5 (10.5)	2.7–3.2 (3.0)
13.	27.1	4.0–4.5 (4.3)	14.5–16.1 (15.5)	3.7–4.0 (3.8)
14.	25.5	4.4–4.9 (4.6)	15.8–17.6 (16.7)	4.0–4.4 (4.2)
15.	29.1	4.5–5.0 (4.7)	16.1–18.0 (17.0)	3.9–4.2 (4.0)
16.	22.0	3.7–4.3 (3.9)	13.2–15.3 (14.0)	3.7–4.1 (3.9)
17.	29.6	(4.1)	(14.6)	(3.5)
18.	32.6	4.8–5.2 (5.0)	17.3–18.5 (17.9)	3.9–4.1 (4.0)
19.	27.4	4.3–5.0 (4.7)	15.3–17.8 (16.8)	3.8–4.3 (4.1)
20.	29.7	4.1–5.4 (4.6)	14.7–19.3 (16.5)	3.6–4.4 (3.9)
21.	29.2	(6.3)	(22.7)	(5.0)
22.	26.4	4.3–4.4 (4.3)	15.6–15.8 (15.6)	(3.9)
23.	30.7	3.8–4.3 (4.1)	13.7–15.6 (14.6)	3.3–3.7 (3.5)
24.	33.2	(3.5)	12.5–12.7 (12.6)	(3.0)
25.	34.7	4.1–4.9 (4.6)	14.6–17.8 (16.4)	3.3–3.9 (3.7)
26.	30.1	3.5–4.7 (4.2)	12.7–16.9 (15.2)	3.2–4.0 (3.7)
27.	33.6	(4.1)	(14.8)	(3.4)
28.	31.0	3.7–3.9 (3.8)	13.3–14.1 (13.7)	3.3–3.4 (3.3)
29.	34.2	3.8–5.0 (4.3)	13.7–18.0 (15.5)	3.2–4.0 (3.5)
30.	29.5	(4.3)	(15.5)	(3.7)
31.	32.4	4.3–4.5 (4.4)	15.6–16.2 (15.8)	3.6–3.7 (3.6)
32.	38.8	3.9–5.0 (4.5)	14.0–18.0 (16.2)	3.1–3.8 (3.5)
33.	29.2	3.2–3.4 (3.3)	11.6–12.3 (11.9)	3.0–3.1 (3.1)
34.	33.4	3.7–4.6 (4.1)	13.3–16.5 (14.9)	3.2–3.7 (3.4)
35.	33.7	(3.9)	(14.0)	(3.3)
36.	28.1	3.8–5.5 (4.9)	13.8–19.8 (17.7)	3.5–4.6 (4.2)

37.	45.6	5.8–6.3 (6.1)	20.9–22.7 (21.9)	4.0–4.2 (4.1)
38.	44.6	(5.7)	(20.4)	(3.9)
39.	37.1	(4.2)	(15.2)	(3.4)
40.	38.1	4.2–4.8 (4.5)	15.0–17.3 (16.2)	3.3–3.7 (3.5)
41.	35.8	3.2–4.9 (4.0)	11.4–17.7 (14.4)	2.7–3.8 (3.3)
42.	39.6	3.4–4.5 (3.9)	12.3–16.0 (14.0)	2.8–3.4 (3.1)
43.	49.3	5.6–6.5 (6.0)	20.0–23.2 (21.6)	3.7–4.2 (3.9)
44.	41.8	2.5–3.3 (3.1)	9.2–12.0 (11.0)	2.2–2.7 (2.5)
*45.	47.4	(1.1)	(4.0)	(1.5)
46.	49.4	(7.8)	(28.2)	(4.9)
47.	58.7	(4.0)	(14.4)	(2.7)
48.	61.5	6.0–7.6 (6.8)	21.8–27.3 (24.4)	3.6–4.3 (4.0)
49.	53.6	6.1–6.6 (6.4)	22.1–23.7 (22.9)	3.9–4.1 (4.0)
50.	54.9	5.0–7.0 (5.7)	18.0–25.0 (20.4)	3.3–4.2 (3.6)
51.	52.0	5.4–5.7 (5.5)	19.4–20.5 (19.9)	3.6–3.7 (3.6)
52.	60.3	6.1–6.5 (6.3)	22.1–23.4 (22.8)	3.7–3.9 (3.8)
53.	53.9	8.2–8.3 (8.2)	29.4–29.9 (29.7)	(4.9)
54.	61.9	(5.1)	(18.5)	(3.2)
55.	54.7	5.0–6.3 (5.7)	18.2–22.6 (20.7)	3.3–3.9 (3.7)
56.	70.0	5.4–7.0 (6.3)	19.6–25.1 (22.6)	3.2–3.9 (3.6)
57.	158.4	4.6–5.0 (4.8)	16.7–18.1 (17.2)	2.1–2.2 (2.1)
Means		4.3–4.8 (4.6)	15.4–17.4 (16.4)	3.5–3.9 (3.7)

*New Quarry trackway.

For each track-maker we show the range and the mean (in parentheses) of speed and relative stride length. A single figure (in parentheses) indicates that only one stride could be measured, or that there was little or no variation in stride length. Figures for the New Quarry track-maker (No. 45) were excluded from calculations of overall means.

equivalent to skeletal hindlimb length. If these estimates were increased by 9% (to provide estimates of H, or 'height of the hindlimb') the mean increment for the ornithopod track-makers would be 3.1 cm; for the coelurosaur track-makers the mean increment would be 1.5 cm. These small increases in estimated body size would not affect the general conclusions that we draw regarding the speeds and gaits of the track-makers.

CARNOSAUR TRACKWAY

In the trackway of the Lark Quarry carnosaur footprint length ranges from 41 cm (estimated) to 64 cm; mean footprint length is 51.4 cm. With the assumptions used by Alexander (1976) *h* could be estimated to lie in the range 1.64 to 2.56 cm — with the mean estimate at 2.06 m. However, it seems legitimate to base our estimate of *h* on the best-preserved and most complete footprint; this particular footprint (number 3 in the trackway) is 64 cm long, providing estimated *h* of 2.56 m. The footprint has a well-defined rear margin, and its length is not exaggerated by scrape-marks; other footprints in the carnosaur trackway appear to have less complete impressions of the rear part of the foot, and they would probably generate underestimates of *h* (and, in consequence, overestimates of the carnosaur's speed).

There are at least two other ways to estimate *h* for the Lark Quarry carnosaur. First it is possible to compare the sizes of carnosaur footprints to the sizes of carnosaur skeletons. Footprints attributed to tyrannosaurs are reported to reach a maximum length of about 80 cm (Haubold 1971), while the largest well-known tyrannosaur, *Tyrannosaurus rex,* has a skeletal hip height about 3.17 m (representing the sum of the lengths of femur, tibia and longest metatarsal). With the admittedly untestable assumption that the largest known footprints were made by animals about the size of *Tyrannosaurus,* skeletal hip height could be predicted as 3.96 times footprint length. In the case of the Lark Quarry carnosaur this method would indicate a skeletal hip height of about 2.54 m.

Next it is possible to make use of the fact that metatarsus length (MT) is strongly correlated with skeletal hip height in carnosaurs — see Fig. 17, where the least squares regression line represents the following allometric equation:

(7) $h \cong 4.15\mathrm{MT} + 28.52$ cm

(In this equation all measurements are expressed in cm; Bartlett's three-group method (see Sokal and Rohlf 1969, p. 483) yields a virtually identical equation). To apply equation (7) in the case of the Lark Quarry carnosaur it is first necessary to estimate MT on the basis of footprint size. It should be possible to make such an estimate with a fair degree of accuracy because in many bipedal dinosaurs MT is roughly equivalent to the summed lengths of phalanges in digit 3 (ΣP; see Figs 6 and 18, and various illustrations given by Coombs 1978); moreover, in a digitigrade animal such as a dinosaur total footprint length (FL) should be slightly greater than ΣP (Fig. 18). In carnosaurs MT seems to be a little greater than ΣP (see Russell 1970, Table 1, for data on Canadian carnosaurs), but would probably have been less than FL (which comprised ΣP, claw sheath, joint capsules and, possibly, a 'heel' region supported by the distal part of the metatarsus). Evidently MT would have been somewhat less than total footprint length. For practical purposes we will assume that MT is roughly equivalent to footprint size index (SI) — which is also less than FL

TABLE 5: ESTIMATES OF SIZE, SPEED AND RELATIVE STRIDE LENGTH FOR 34 *SKARTOPUS* TRACK-MAKERS.

	estimated h (cm)	estimated speed (m/s)	(km/h)	estimated λ/h
1.	13.3	3.0–4.2 (3.7)	10.8–15.1 (13.3)	3.8–5.0 (4.5)
2.	13.3	3.8–4.4 (4.2)	13.6–15.9 (15.0)	4.6–5.2 (4.9)
3.	14.4	2.8–3.3 (3.1)	10.2–12.0 (11.2)	3.6–4.0 (3.8)
4.	14.5	3.2–3.9 (3.5)	11.4–14.0 (12.6)	3.9–4.5 (4.2)
5.	14.8	3.5–4.1 (3.8)	12.5–14.7 (13.6)	4.1–4.7 (4.4)
6.	14.9	2.8–3.4 (3.0)	10.2–12.2 (10.8)	3.5–4.0 (3.7)
7.	15.0	2.9–3.3 (3.1)	10.6–11.9 (11.2)	3.6–3.9 (3.8)
8.	15.1	3.4–3.6 (3.5)	12.1–13.0 (12.5)	4.0–4.2 (4.1)
9.	15.2	3.1–3.8 (3.4)	11.3–13.8 (12.3)	3.8–4.4 (4.0)
10.	15.3	2.8–3.5 (3.0)	10.1–12.5 (10.9)	3.4–4.1 (3.7)
11.	15.5	3.3–3.4 (3.3)	11.8–12.3 (12.1)	3.9–4.0 (3.9)
*12.	15.5	3.4–3.6 (3.4)	12.1–12.8 (12.4)	3.9–4.1 (4.0)
13.	15.5	3.6–4.1 (3.9)	12.8–14.9 (14.0)	4.1–4.6 (4.4)
14.	15.6	3.4–3.8 (3.6)	12.2–13.5 (13.0)	4.0–4.3 (4.2)
15.	16.2	3.6–3.9 (3.7)	12.9–13.9 (13.3)	4.1–4.3 (4.2)
16.	16.3	2.8–3.2 (3.0)	10.2–11.4 (10.6)	3.4–3.7 (3.5)
17.	16.4	3.1–3.3 (3.2)	11.3–11.8 (11.6)	3.7–3.8 (3.7)
18.	16.6	3.3–3.5 (3.4)	11.9–12.4 (12.1)	3.8–3.9 (3.8)
19.	16.6	(3.2)	(11.4)	(3.7)
20.	17.2	2.5–3.7 (3.1)	8.8–13.3 (11.3)	3.0–4.1 (3.6)
21.	17.7	2.8–3.9 (3.3)	9.9–13.9 (12.0)	3.2–3.8 (3.7)
22.	17.9	3.1–3.9 (3.3)	11.0–14.1 (12.0)	3.5–4.2 (3.7)
23.	17.9	2.5–3.1 (2.8)	9.0–11.3 (10.1)	3.0–3.5 (3.2)
24.	18.2	2.3–3.2 (2.6)	8.3–11.6 (9.5)	2.8–3.6 (3.1)
25.	18.2	2.2–2.8 (2.5)	8.0–10.2 (9.1)	2.7–3.2 (3.0)
26.	18.3	(3.2)	(11.7)	(3.6)
27.	18.5	2.6–2.8 (2.7)	9.4–10.1 (9.7)	3.0–3.2 (3.1)
28.	19.3	2.9–3.5 (3.2)	10.4–12.6 (11.4)	3.2–3.7 (3.5)
29.	19.3	2.5–2.6 (2.5)	8.9–9.3 (9.1)	2.9–3.0 (2.9)
30.	19.6	2.7–2.9 (2.8)	9.8–10.5 (10.1)	3.1–3.2 (3.1)
31.	19.9	3.2–3.7 (3.5)	11.7–13.2 (12.6)	3.5–3.8 (3.7)
32.	20.1	2.6–3.0 (2.8)	9.2–10.7 (10.1)	2.9–3.2 (3.1)
33.	21.6	2.5–3.1 (2.9)	9.1–11.3 (10.3)	2.8–3.3 (3.1)
34.	21.9	2.7–3.4 (3.0)	9.6–12.2 (10.6)	2.9–3.5 (3.1)
Means		3.0–3.5 (3.2)	10.7–12.5 (11.6)	3.5–3.9 (3.7)

For each track-maker we show the range and the mean (in parentheses) of speed and relative stride length. A single figure (in parentheses) indicates that only one stride could be measured, or that there was little or no variation in stride length.

* Trackway No. 12 was made by an animal with consistent 'flat-footed' gait (see Plate 14, fig. B). The length of each footprint is exaggerated by an imprint of the metatarsus, and to estimate the animal's size and speed our measurements of total footprint length were reduced by 50%.

because the footprint is longer than wide. The best-preserved carnosaur footprint at Lark Quarry has SI of 57.69 cm; by substituting this figure for MT in equation (*7*) we can estimate skeletal hip height to have been about 2.68 m.

These various estimates are in close agreement, and they indicate that the Lark Quarry carnosaur was between 2.54 and 2.68 metres in height at the hip. The mean figure, which we will use for estimating the animal's speed, is 2.59 m. Apparently the animal was about the same size as one specimen of the Canadian carnosaur *Albertosaurus libratus* (National Museum of Canada, No. 2120, with h about 2.63 m; Lambe 1917); it would have been intermediate in size between specimens of *Daspletosaurus torosus* (h 2.40 m, estimated from data of Russell 1970) and *Tyrannosaurus rex* (h about 3.17 m; Osborn 1917).

The strides of the Lark Quarry carnosaur range in length from 2.82 m to 3.74 m (mean 3.31 m). Consequently relative stride length (λ/h) is estimated to range from 1.09 to 1.44 (mean 1.28). In every stride λ/h is well below 2.0, which indicates that the animal was using a walking gait (Alexander 1976) and that its speed is most appropriately estimated with equation (*6*). The carnosaur's progress may be plotted in some detail, as follows:

stride	speed (m/s)	speed (km/h)	λ/h
1	2.34	8.43	1.44
2	2.13	7.65	1.36
3	2.35	8.47	1.44
4	2.34	8.43	1.44
5	1.76	6.32	1.21
6	1.67	6.03	1.18
7	1.74	6.26	1.20
8	1.54	5.54	1.12
9	1.47	5.28	1.09
means	1.93	6.93	1.28

The animal took a slightly weaving course (Fig. 3), during which it showed a definite tendency to decelerate (i.e. to shorten its strides). Its first four strides are relatively long and are defined by very deep footprints; the animal then switched quite abruptly to a series of shorter strides (Nos. 5–9, Fig. 22A) and its footprints became noticeably shallower. The last two strides are the shortest and were taken as the animal made a sharp turn to its right.

ORNITHOPOD TRACKWAYS

In our preliminary account of Lark Quarry (1979) the makers of the ornithopod trackways (*Wintonopus*) were estimated to range from the size of bantams to the size of ostriches; their mean speed was calculated to be about 4.31 m/s (15.52 km/h). These preliminary estimates of size and speed were derived from a small sample (parts of 10 trackways) with the methods described by Alexander (1976).

In the 57 trackways studied here mean footprint length ranges from 2.40 cm to 22.75 cm (mean 6.68 cm); by excluding the earlier-formed trackway of the exceptionally large animal (No. 57 in Table 4) the range of means for footprint length is reduced to 2.40 — 10.86 cm (with overall mean 6.39 cm). Alexander assumed (1976) that height at the hip (h) could be estimated as approximately four times footprint length for a variety of dinosaurian track-makers; if we apply this assumption to the *Wintonopus* data the track-makers are estimated to have had h ranging between 9.60 and 43.44 cm (mean 25.58 cm), with the single large individual at 91.0 cm. However, Alexander indicated that footprint length (FL) could represent anything between $0.23h$ and $0.28h$ in the bipedal dinosaurs that he studied (1976), and it seems worthwhile to investigate an alternative method for estimating h.

Analysis of variance (p. 424) revealed considerable variation in footprint length within the *Wintonopus* trackways. Within a single trackway there may occur foreshortened ('stubby-toed') prints, normal prints and attenuated toe scratches from a single foot (Figs 5L and 7, Pl. 10D). Consequently mean footprint length for a trackway may not be a satisfactory indicator of the track-maker's size — because the mean will be affected by the relative frequencies of foreshortened and attenuated footprints. Fortunately footprint size index (SI) seems to be a reliable guide to the relative sizes of two or more track-makers: the index differs from one trackway to the next, but is virtually constant within any one trackway. Footprint size index is usually a little greater than footprint length in *Wintonopus* (because the footprints are usually broader than long), and it has the following range: 2.89 to 12.69 cm (mean 6.74 cm), with the single large individual at 26.59 cm. Two observations make it possible to estimate h on the basis of SI: first, in the foot skeletons of many ornithopods the summed lengths of phalanges in digit 3 (ΣP) is roughly equal to the length of metatarsal 3 (MT; see Figs 6A, C); and, second, there exists a strong correlation between MT and skeletal hip height in ornithopods (see Fig. 19). So, to calculate h for the *Wintonopus* track-makers there seems to be only one prerequisite —

an estimate of MT (or of ΣP) derived from SI. By dinosaurian standards the *Wintonopus* track-makers seem to have been fairly small animals, so that absolute differences between FL and ΣP (and hence MT) are likely to have been small. For the sake of convenience we will assume that SI is roughly equal to MT. It may be noted that SI is usually a little greater than FL, because the *Wintonopus* footprints are normally a little broader than long. Consequently our estimates of *h* (based on SI) will tend to be slightly greater than similar estimates based on FL. This difference will, on the whole, have a conservative effect — in the sense that the sizes of track-makers may overestimated, and their speeds may be underestimated.

Figure 19A shows the relationship between MT and skeletal hip height in a sample of 32 ornithopod skeletons (with MT ranging from 6.3 to 38.1 cm); the least squares regression line represents the following allometric equation:

(8) $h \cong 3.76\mathrm{MT}^{1.16}$

where both *h* and MT are expressed in centimetres. By substituting SI for MT in this equation we estimate that the Lark Quarry ornithopods ranged in skeletal hip height from 12.86 to 71.57 cm (mean 34.41 cm), with the solitary large individual at 168.81 cm. However, the regression equation for cursorial ornithopods (with femur shorter than tibia) is slightly different from that for graviportal ornithopods (with femur longer than tibia); for cursorial ornithopods the equation is:

(9) $h \cong 3.97\mathrm{MT}^{1.08}$

while for graviportal ornithopods it is:

(10) $h \cong 5.06\mathrm{MT}^{1.07}$

The two regression lines, which are shown in Fig. 19B, have similar slopes but different intercepts. In general terms equation (*10*) provides estimates of *h* about 20 to 25% greater than those derived with equation (*9*). The Lark Quarry ornithopods seem to have been small animals, judging from the size of their footprints,and this might indicate that equation (*9*), based on data from cursorial ornithopods, should be used to estimate *h*. It must be admitted, however, that the exact identity of the *Wintonopus* track-makers is unknown — beyond that fact that they seem to have been ornithopods of some sort. For this reason we have obtained three estimates of *h* for each track-maker (by substituting SI for MT in each of the preceding equations), and we will use the mean figure in calculating the speed of each animal. These mean values for *h* range from 13.70 to 69.98 cm (overall mean 34.82 cm), excluding the single large animal with *h* estimated to be 158.59 cm.

Of the 57 *Wintonopus* trackways examined here only one appears to have been made by an animal more than 1 metre high at the hip. Forty-six of the track-makers (81%) are estimated to have *h* less than 50 cm, and 24 of them (42%) *h* less than 30 cm. In all cases Alexander's assumptions (1976) would provide smaller estimates of *h*.

In terms of general body size the Lark Quarry animals may be compared with cursorial ornithopods of the families Fabrosauridae, Hypsilophodontidae and Heterodontosauridae (see skeletal reconstructions or flesh restorations given by Galton 1974, Thulborn 1972, Santa Luca et al. 1974); they might also be compared with juvenile specimens of some bigger graviportal ornithopods (e.g. the juvenile hadrosaurs described by Horner and Makela 1979) and with the juvenile psittacosaurs recently described by Coombs (1980a, 1982). From the evidence of trackways it does not seem possible to decide with certainty whether the Lark Quarry ornithopods were small cursorial forms ranging up to adult status, or whether they were juveniles of some bigger graviportal ornithopod. Neither of these possibilities can be dismissed entirely: two types of small ornithopod, resembling hypsilophodontids, are reported from the Cretaceous of Victoria (Flannery and Rich 1981), and a large ornithopod with *h* about 2.44 m was recently described from the Lower Cretaceous of Queensland (*Muttaburrasaurus,* Bartholomai and Molnar 1981). In either case it would still seem reasonable to regard the smallest (at least) of the Lark Quarry track-makers as juvenile animals. It has sometimes been supposed that juvenile dinosaurs were rare (Richmond 1965, Leonardi 1981), but Horner and Makela (1979) found that more than 80% of dinosaur specimens collected from the Two Medicine Formation (Upper Cretaceous) of Montana could be identified as juveniles or subadults. It seems that juvenile dinosaurs may have been quite common, at least in some localities.

The curve illustrating size frequency distribution for the *Wintonopus* track-makers is distinctly skewed and is similar to the type of curve derived by Boucot (1953) from 'life assemblages' of fossils (see Fig. 21A). The curve might be interpreted in any of several ways. First it could simply be regarded as a survivorship curve for a population of small cursorial ornithopods. According to this interpretation the animals would normally have grown to achieve h of about 30 cm (peak of curve); thereafter the mortality rate would have reached its maximum (steepest part of curve), with fewer and fewer animals surviving to reach greater and greater size (by virtue of the indeterminate growth prevailing among reptiles). This interpretation assumes, of course, that the sample of 57 track-makers is truly representative of the dinosaur population from which it was drawn; it also assumes the existence and constancy of some strong correlation between size and age. Secondly it is possible to interpret Fig. 21A as a survivorship curve based on a sample drawn from a population of big graviportal ornithopods (with assumptions as above). In this case it would appear that there was a high rate of mortality among juveniles or subadults once these had attained h of about 40 cm. The adults, presumably with h of 1.5 metres or more, would then have been comparatively rare and relatively long-lived. Next there is the possibility that our sample of 57 track-makers is not a representative one: it could comprise animals from two or more species, or there could be serious under-representation of bigger animals in a single species. (It seems scarcely possible that smaller animals could be under-represented). There is no obvious reason to assume that the *Wintonopus* trackways were produced by two or more different types of dinosaur: none of the frequency distributions is strongly bimodal (Figs 8 and 9), there are impressive correlations between any two dimensions of the footprints and trackways (Fig. 10), and all the footprints can be interpreted as those of animals sharing one distinctive pattern of foot structure (Fig. 6C) and using the same gait (Fig. 11). We cannot discount entirely the possibility that our sample of 57 *Wintonopus* trackways might be heterogeneous (in which case we could deduce nothing about the population structure and possible affinities of the track-makers), but this possibility does seem rather unlikely: it supposes the co-existence of two or more dinosaurian species, each of which is represented by juveniles or is characteristically of small size, and each of which produced *Wintonopus* -like trackways. The final possibility is that bigger animals did exist, but that they are under-represented in our sample. Under-representation of bigger animals could not be regarded as an effect of sampling: trackways of large animals are not common at Lark Quarry, and we ensured that our sample contained data from the largest and second-largest examples of *Wintonopus*. Consequently this final possibility must imply that large and small animals were segregated, either fortuitously or through some deliberate strategy on the part of the potential track-makers. Of all these possible interpretations the simplest would certainly seem to be the first — that the sample of 57 trackways is representative of a dinosaur population in which animals rarely grew to hip heights estimated at greater than 70 cm. Finally there is some evidence of three size classes in the *Wintonopus* sample (note the three clumps of data points in Fig. 10). In terms of estimated hip height these three size classes have approximate limits of 13 to 20 cm, 25 to 40 cm, and 50 to 60 cm. There is no way to investigate the possibility that these size groupings might be equivalent to age classes.

From our estimates of h it is calculated that the mean value of λ/h per trackway ranges from 2.69 to 5.03 (overall mean 3.69); these figures exclude values for the solitary large animal (λ/h 2.10), and for the New Quarry track-maker. It seems that all the *Wintonopus* track-makers at Lark Quarry were using a gait faster than a walk (λ/h greater than 2.0). Two individuals were apparently moving at a trot or a slow run (with mean λ/h at 2.1 and 2.7), whereas all the others (96%) were using a fast running gait equivalent to a mammalian gallop (with λ/h at 3.0 or greater).

The 56 ornithopod track-makers at Lark Quarry all have λ/h estimated to be greater than 2.0, so that their speeds are most appropriately estimated by means of equation (*2*) re-written as:

$$u \cong [gh(\lambda/1.8h)^{2.56}]^{0.5} \tag{11}$$

In this equation λ and h are expressed in metres and u is in metres per second. Mean speed per trackway is estimated to range from 2.92 m/s (10.52 km/h) to 8.24 m/s (29.66 km/h), with the overall mean for 55 animals (excluding solitary large individual) at 4.48 m/s (16.12 km/h). The one exceptionally large animal has an estimated mean speed of 4.78 m/s (17.22 km/h). The minimum speed estimated for any of these track-makers, on the basis of its single shortest stride, is 2.22 m/s (8.00 km/h); the maximum speed estimated for any of the track-makers, on the basis of its single longest stride, is 8.30 m/s (29.88 km/h).

The single *Wintonopus* trackway at New Quarry has mean SI of 8.91 cm; for this track-maker h is estimated to have been 47.4 cm, indicating λ/h of about 1.54. The New Quarry animal was not associated with those at Lark Quarry, and it seems to have been using a different gait (walking rather than running). Its speed, which is best calculated with equation (*6*), is estimated to have been 1.11 m/s (3.98 km/h).

Even if its speed is estimated, inappropriately, with equation (*11*) the New Quarry animal would still seem to have been moving more slowly than any of the Lark Quarry track-makers (i.e. at 1.76 m/s, or 6.34 km/h).

The estimated sizes, speeds and relative stride lengths of all 57 *Wintonopus* track-makers are summarized in Table 4. The animals seem to have maintained fairly constant speeds, and in most cases mean stride length for the second half of the trackway differs only slightly from mean stride length for the first half (see Fig. 23A). On average the difference between these two means in an increase of 1.3%. An analysis of stride lengths in the longest section of ornithopod trackway (No. 41 in Table 4, comprising 17 strides) reveals no consistent trend towards acceleration (lengthening of strides) or deceleration (shortening of strides). Mean stride length for the second half of this trackway is 6.8% less than mean stride length for the first half. Short sections of this trackway (Fig. 22B) might give the impression of a strong tendency to lengthen or shorten the strides, yet the track-maker seems, overall, to have maintained a reasonably consistent stride length (116.82 ± 11.13 cm; CV 9.5%).

To summarize, the *Wintonopus* trackways at Lark Quarry seem to have been made by small ornithopod dinosaurs, mostly less than 60 cm in height at the hip. All these dinosaurs seem to have been using a fast running gait, with λ/h in most cases between 3.2 and 4.1. For the majority speeds are estimated between 3.4 m/s (12.2 km/h) and 5.6 m/s (20.2 km/h), and there is no clear evidence that the animals were accelerating or decelerating.

Coelurosaur trackways

In our preliminary study of Lark Quarry (1979) we estimated that the makers of the coelurosaur trackways (*Skartopus*) had a size range equivalent to that between bantams and half-grown emus; their mean speed was estimated to have been about 3.62 m/s (13.04 km/h). These preliminary estimates of size and speed were obtained by applying Alexander's method (1976) to parts of 10 trackways.

With Alexander's working assumption (1976) that footprint length (FL) represents about $0.25h$ it may be estimated that the 34 trackways studied here were made by animals ranging from 14.5 to 22.5 cm in height at the hip (overall mean 17.8 cm). But again, as with the ornithopod track-makers, it may be worthwhile to investigate another method for estimating h.

Analysis of variance (p. 429) reveals that FL is highly variable within and among the *Skartopus* trackways; so, too, are footprint width (FW) and footprint size index (SI). Consequently there seems to be little advantage in selecting SI, rather than FL or FW, as an indicator to the relative sizes of the track-makers. None of these variables appears to be a very reliable guide to the relative sizes of the track-makers, but this fact is not particularly important because all these animals seem to have been much the same size anyway. Our estimates of size and speed for the track-makers will be based on mean FL per trackway. It might not be appropriate to base these estimates on mean SI (as was done for the ornithopod trackways) because this is usually less than actual footprint length — on account of the footprints usually being longer than broad. This preference for FL, rather than SI, will have a conservative effect — in that estimates of h will tend to be increased and estimates of speed will tend to be decreased. In the 34 trackways studied here mean FL ranges from 3.62 to 5.62 cm, with the overall mean at 4.46 ± 0.50 cm.

In a variety of coelurosaurs MT (the length of metatarsal 3) is strongly correlated with skeletal hip height; this relationship illustrated in Fig. 20, where the least squares regression line represents the following allometric equation:

$$(12) \qquad h \cong 3.06\mathrm{MT}^{1.14}$$

Both MT and h are expressed in centimetres. To estimate h for the Lark Quarry coelurosaurs we will substitute FL for MT in this equation, on the assumption that these two dimensions were roughly equal. This assumption is reasonable because both dimensions were probably a little greater than ΣP (summed lengths of phalanges in digit 3). The slight preponderance of FL over ΣP is apparent from Fig. 18; from various illustrations of coelurosaur foot skeletons it appears that MT is also a little greater than ΣP — in a ratio about 11:10 (see Figs 6D, E, and references given in caption to Fig. 20).

By substituting FL for MT in equation (*12*) we estimate that the Lark Quarry coelurosaurs ranged from 13.27 cm to 21.93 cm in height at the hip (with mean for the 34 animals at 16.92 ± 2.23 cm). These estimates are slightly smaller than those obtained with Alexander's assumption that h is approximately four times FL; for the smallest track-maker the two estimates differ by 12 mm, and for the largest they differ by 6 mm. These differences are unlikely to be of great significance, especially since Alexander's work (1976) indicates that h could represent anything from about 3.6FL to about 4.3FL in the various bipedal dinosaurs that he studied. Moreover these differences will not affect the general conclusions that we draw regarding the gaits and speeds of the track-makers (see Table 6, where our estimates for h are increased by about 40 to 50%).

From these estimates is seems that the *Skartopus* track-makers were somewhat smaller than the familiar coelurosaurs *Coelophysis* (h from 33.7 to 55.9 cm in 13 specimens listed by Colbert 1964), *Ornitholestes* (h about 48.3 cm, Osborn 1917) and *Podokesaurus* (h 25.5 cm, Talbot 1911). The only well known coelurosaur of comparable size would seem to be *Compsognathus,* with h as little as 21.1 cm (for holotype, estimated from measurements given by Ostrom 1978). However, the *Skartopus* footprints do agree in size with many other footprints attributed to coelurosaurs (see Table 2).

The size frequency distribution for the *Skartopus* track-makers is distinctly skewed (Fig. 21B) and is open to the several interpretations that were considered earlier for the *Wintonopus* track-makers. The possible interpretations may be summarized as follows:

1. The 34 *Skartopus* track-makers represent a coelurosaur population in which individual animals grew to a maximum hip height estimated at 22 cm. This interpretation assumes that the sample of 34 track-makers is truly representative of the population from which it was drawn (i.e. that it includes both juveniles and adults), and that there existed a strong unvarying correlation between size and age.

2. The 34 track-makers are juveniles of some type of theropod dinosaur that grew to greater size — though the bigger individuals are not represented at Lark Quarry. This implies that large and small animals were segregated, either by chance or through their behaviour.

3. The sample of 34 trackways is heterogeneous. This assumes that two or more types of small (or juvenile) dinosaurs made identical trackways at a single site, and that they did so at approximately the same time.

All these possible interpretations involve untestable assumptions, but the first of them would seem to be the simplest. In any case it is noteworthy that the *Skartopus* track-makers must have been remarkably small animals by dinosaurian standards. Even if it is assumed that the track-makers were exceptionally long-legged animals resembling ornithomimids (or 'ostrich dinosaurs') it may be estimated that the largest of them was less than 32 cm in height at the hip (see Table 6 and further discussion below).

With our estimates of h the mean value of λ/h per *Skartopus* trackway is found to range from 2.90 to 4.94, with the overall mean at 3.71. In only three trackways is minimum λ/h (based on the shortest stride) estimated to be less than 2.9, and in no case does it fall below 2.7. Evidently all 34 track-makers were using a fast running gait. These figures for λ/h indicate that the speeds of the track-makers are most appropriately estimated by means of equation (*11*). Mean speed per trackway is estimated to range from 2.53 m/s (9.09 km/h) to 4.16 m/s (14.98 km/h), with the overall mean at 3.22 m/s (11.58 km/h). The minimum speed estimated for any of the track-makers, on the basis of its single shortest stride, is 2.23 m/s (8.03 km/h); the maximum speed estimated for any of the track-makers, on the basis of the single longest stride, is 4.42 m/s (15.91 km/h).

Table 5 presents a summary of estimated size, speed and relative stride length for each of the 34 track-makers. There is no clear indication that the animals were either accelerating or decelerating. In most cases mean stride length for the second half of a trackway differs only slightly from mean stride length for the first half (Fig. 23B). On average this difference between the two means is a decrease of about 2.1%. From Fig. 23B it appears that the majority of track-makers showed a slight reduction in stride length during their progress. However, this tendency to shorten the strides is neither consistent nor well-marked, and it is probably of little significance. By way of illustration Fig. 22C shows an analysis of the longest section of coelurosaur trackway (No. 20 in Table 5, comprising 22 strides): in the latter half of this trackway mean stride length is 2.5% less than mean stride length in the first half, but there is no consistent trend towards progressive shortening of the strides. Short sections of the trackway could give the impression of a strong trend to shortening or lengthening the strides, yet the track-maker seems, overall, to have maintained a fairly consistent stride length (61.77 ± 5.40 cm; CV 8.7%).

In summary, the *Skartopus* trackways seem to have been produced by small coelurosaurs, all of which are estimated to have been less than 22 cm high at the hip. All of these animals seem to have been using a fast running gait; estimates of λ/h are in most instances greater than 2.9, though a few trackways include short strides indicating occasional lapses of λ/h as low as 2.7. Mean

TABLE 6: Estimates of Size, Speed and Relative Stride Length for 34 *Skartopus* Track-Makers — With the Assumption That These Were Animals Resembling Ornithomimids. Ranges and Means of Estimates Shown as in Table 5.

	h (cm)	speed (m/s)	speed (km/h)	λ/h
1.	19.5	2.2–3.1 (2.8)	8.0–11.1 (9.9)	2.6–3.4 (3.1)
2.	19.6	2.8–3.3 (3.1)	10.1–11.8 (11.1)	3.1–3.5 (3.4)
3.	20.9	2.1–2.5 (2.3)	7.6–8.9 (8.4)	2.4–2.8 (2.6)
4.	21.1	2.4–2.9 (2.6)	8.5–10.4 (9.4)	2.7–3.1 (2.9)
5.	21.5	2.6–3.0 (2.8)	9.4–10.9 (10.2)	2.8–3.2 (3.0)
6.	21.6	2.1–2.5 (2.3)	7.6–9.1 (8.1)	2.4–2.8 (2.5)
7.	21.7	2.2–2.5 (2.3)	7.9–8.9 (8.3)	2.5–2.7 (2.6)
8.	21.9	2.5–2.7 (2.6)	9.0–9.7 (9.4)	2.7–2.9 (2.8)
9.	22.0	2.3–2.9 (2.6)	8.4–10.3 (9.2)	2.6–3.0 (2.8)
10.	22.1	2.1–2.6 (2.3)	7.5–9.3 (8.2)	2.4–2.8 (2.5)
11.	22.4	2.5–2.6 (2.5)	8.9–9.2 (9.1)	2.7–2.8 (2.7)
*12.	22.4	2.5–2.8 (2.6)	9.0–9.6 (9.3)	2.7–2.9 (2.8)
13.	22.4	2.7–3.1 (2.9)	9.6–11.2 (10.5)	2.9–3.2 (3.1)
14.	22.6	2.6–2.8 (2.7)	9.2–10.2 (9.8)	2.8–3.0 (2.9)
15.	23.2	2.7–2.9 (2.8)	9.7–10.5 (10.0)	2.8–3.0 (2.9)
16.	23.4	2.1–2.4 (2.2)	7.7–8.5 (8.0)	2.4–2.6 (2.4)
17.	23.5	2.4–2.5 (2.4)	8.5–8.9 (8.7)	(2.6)
18.	23.8	2.5–2.6 (2.5)	9.0–9.4 (9.1)	(2.7)
19.	23.8	(2.4)	(8.6)	(2.6)
20.	24.6	1.9–2.8 (2.4)	6.7–10.0 (8.5)	2.1–2.8 (2.5)
21.	25.3	2.1–2.9 (2.5)	7.5–10.6 (9.1)	2.3–2.9 (2.6)
22.	25.4	2.3–3.0 (2.5)	8.4–10.7 (9.1)	2.4–2.9 (2.6)
23.	25.4	1.9–2.4 (2.1)	6.8–8.5 (7.7)	2.1–2.5 (2.3)
24.	25.8	1.7–2.4 (2.0)	6.3–8.8 (7.2)	1.9–2.5 (2.2)
25.	25.9	1.7–2.1 (1.9)	6.1–7.7 (6.9)	1.9–2.3 (2.1)
26.	26.0	(2.5)	(8.9)	(2.5)
27.	26.2	2.0–2.1 (2.0)	7.2–7.7 (7.4)	2.1–2.3 (2.2)
28.	27.2	2.2–2.7 (2.4)	7.9–9.6 (8.7)	2.3–2.6 (2.5)
29.	27.3	1.9–2.0 (1.9)	6.8–7.1 (6.9)	2.0–2.1 (2.0)
30.	27.6	2.1–2.2 (2.2)	7.5–8.0 (7.8)	2.2–2.3 (2.2)
31.	27.9	2.5–2.8 (2.7)	8.9–10.1 (9.7)	2.5–2.7 (2.6)
32.	28.2	2.0–2.3 (2.1)	7.1–8.2 (7.7)	2.1–2.3 (2.2)
33.	30.1	1.9–2.4 (2.2)	7.0–8.7 (8.0)	2.0–2.4 (2.2)
34.	30.5	2.1–2.6 (2.3)	7.4–9.4 (8.2)	2.1–2.5 (2.2)
Means		2.3–2.6 (2.4)	8.1–9.5 (8.7)	2.4–2.7 (2.5)

estimated speeds of the track-makers are generally in the range 2.82 m/s to 3.61 m/s (10.16 to 13.00 km/h), and there is no clear indication that the animals were either accelerating or decelerating.

The preceding estimates of size and speed depend on the assumption that the Lark Quarry track-makers had hindlimb proportions similar to those in 'typical' coelurosaurs such as *Coelophysis, Compsognathus* and *Ornitholestes*. However, one group of small to medium-sized theropod dinosaurs — the ornithomimids or 'ostrich dinosaurs' — is characterized by unusual hindlimb proportions: these animals have exceptionally long hindlimbs terminating in relatively short toes. For the sake of completeness we will examine the possibility that *Skartopus* trackways might have been made by animals resembling ornithomimids.

From published measurements of ornithomimid skeletons (Russell 1972 — *Ornithomimus, Struthiomimus, Dromiceiomimus;* Osmólska et al. 1972 — *Gallimimus*) it appears that MT represents something between 1.45 and 1.72 times ΣP (the mean figure derived from 9 specimens being 1.57). Since FL was probably a little greater than ΣP (see Fig. 18) we may assume, for the sake of convenience, that MT was equivalent to about 1.5FL. From the same osteometric data it seems that there is a strong positive correlation between MT and skeletal hip height (r = 0.997, N = 9); the latter may be predicted by means of the following allometric equation:

$$h \cong 3.49\mathrm{MT}^{1.02} \qquad (13)$$

where h and MT are expressed in centimetres. If the Lark Quarry coelurosaurs resembled ornithomimids in limb proportions their skeletal hip heights might, then, be estimated as follows:

$$h \cong 3.49(1.5\mathrm{FL})^{1.02} \qquad (14)$$

This method provides estimates of h ranging from 20.44 to 31.96 cm (with overall mean of 25.27 cm). Consequently estimates of mean λ/h per trackway would range from 1.96 to 2.88 (with overall mean 2.49). In only two of the 34 cases would the estimate for mean λ/h be less than 2.0 (actually 1.99 and 1.96). These figures would indicate that all the *Skartopus* track-makers were trotting or running (or, in two cases, were at least on the point of breaking into a trot). Estimates of mean speed per trackway, obtained with equation (*11*), range from 1.85 m/s to 2.97 m/s (6.67 km/h to 10.69 km/h), with the overall mean at 2.33 m/s (8.40 km/h). These particular estimates of size, speed and relative stride length are summarized in Table 6.

It seems difficult to escape the conclusion that *Skartopus* trackways are those of running dinosaurs — even with the assumption that these might have been exceptionally long-legged dinosaurs resembling ornithomimids. There are at least two good reasons for believing that the track-makers were not ornithomimids. First there is simply the matter of size: the *Skartopus* footprints are much smaller than the foot skeleton in any specimen of ornithomimid dinosaur so far described. In the smallest of the complete foot skeletons listed by Osmólska et al. (1972, p. 131) ΣP is 12.8 cm. One smaller example is listed by these authors, but it lacks the penultimate phalanx in digit 3; for this specimen we estimate ΣP to have been about 9.0 cm. In the ornithomimids described by Russell (1972) ΣP ranges from 21.5 cm to more than 25.5 cm. Footprints attributed to ornithomimids, or to unknown but presumably similar dinosaurs, have FL from about 10 cm (*Hopiichnus shingi,* Welles 1971) to about 28 cm (*Ornithomimipus angustus,* Sternberg 1926). By comparison the largest figure for mean FL in any of the *Skartopus* trackways is 5.62 cm. In the second place there seem to be no certainly-identified skeletal remains of ornithomimids from the Gondwana continents. A few bones (dorsal vertebrae and a phalanx) from the Lameta Formation of India were described by von Huene and Matley (1933) as *Ornithomimoides mobilis* and *O. barasimlensis,* but Osmólska et al. regarded the material as 'systematically insufficient' (1972, p. 104). Russell (1972) considered the two species to be *nomina vana.* Molnar (1980), examining these and other records, concluded that there was no evidence suggesting that ornithomimids existed on the southern continents. In summary, the *Skartopus* footprints seem rather too small to be those of ornithomimids, and there is little evidence to suggest that such dinosaurs existed in the southern continents. Consequently we may assume the Lark Quarry trackways to have been made by some other type of theropod dinosaur — which presumably had 'typical' limb proportions.

A DINOSAUR STAMPEDE?

The most distinctive features of the Lark Quarry trackway site are: (1) that the dinosaurian track-makers were very numerous; (2) that nearly all these track-makers seem to have been small by dinosaurian standards; (3) that trackways of the two main types (*Wintonopus* and *Skartopus*) are in some places coincident, superimposed or interwoven; (4) that all the trackways (except that of the carnosaur) head in a single direction; and (5) that all the track-makers (except the carnosaur) seem to have been running. This combination of features appears to be unique, and it previously led us to interpret the Lark Quarry trackways as the result of a dinosaurian stampede (Thulborn and Wade 1979). The evidence underlying this interpretation may now be examined in more detail.

The Lark Quarry bedding plane carries one of the densest accumulations of dinosaur footprints yet reported (see Table 7). In our preliminary description of the site we estimated that these footprints represented the trackways of at least 130 dinosaurs (excluding the carnosaur), with coelurosaurs (= *Skartopus* trackways) outnumbering ornithopods (= *Wintonopus* trackways) in a ratio about 55:45. It proved impossible to assign every footprint at Lark Quarry to a particular trackway, and so our estimate for the number of track-makers must be checked in some other way. In a 1 metre wide transect at a right angle to the direction of the trackways (between points X–X in Fig. 3) we counted a total of 350 footprints. In practically all cases mean pace length for a track-maker (whether ornithopod or coelurosaur) is less than 1 metre — which means that nearly every animal crossing the line of the transect should have left at least one footprint in the metre-wide strip. Consequently the *maximum* number of animals that crossed the transect could be estimated at

350. However, mean pace length for *Wintonopus* is 68 cm (i.e. about 1½ footprints per metre), and for *Skartopus* it is 32 cm (i.e. about 3 footprints per metre). By assuming that ornithopods and coelurosaurs were present in equal numbers we can estimate the number of animals to have crossed the transect as:

$$\frac{350}{(3 \times 0.5) + (1.5 \times 0.5)} = 156 \text{ animals}$$

This very rough estimate must be regarded as an absolute minimum. We suspect that coelurosaurs outnumbered ornithopods, but it is impossible to make allowance for this without identifying every footprint and assigning to it a particular trackway. This proved an impossible task (for reasons described earlier; see p. 418). Moreover it is certain that many smaller animals (both coelurosaurs and ornithopods) crossed our transect without leaving recognizable footprints: these animals would have been so light that their broad-spreading and rather springy feet simply failed to break through the surface of the sediment. This seems to have happened very commonly, to judge from the number of discontinuities or 'gaps' in the trackways at Lark Quarry. The area of bedding plane exposed at Lark Quarry is delimited partly by erosion and partly by undisturbed overburden (mainly to S and SW, see Pl. 3). Within this area the footprints are fairly evenly distributed (Pl. 4), and it seems almost certain that more of them could be revealed by extending the quarry to the SSW. Our estimate of 156 animals may well represent a fraction of the number of dinosaurs that traversed Lark Quarry and its environs.

Trackways are certainly abundant, but this fact alone does not support the hypothesis of a dinosaur stampede. However, this fact does assume some significance when one considers that all the trackways may have been formed simultaneously by animals running in a single direction.

There are several reasons for believing that all the *Wintonopus* and *Skartopus* trackways at Lark Quarry were formed at, or about, the same time (excepting the single unusually large example of *Wintonopus*). First, all these trackways are very similar in preservation; there is no evidence (such as scouring or erosion) to indicate that some tracks are much older than others. Second, all the trackways are impressed to about the same depth — evidently in sediment of uniform consistency. If the trackways had accumulated over a lengthy period one might expect to find evidence of a change in the consistency of the substrate (i.e. some tracks more deeply impressed than others). Finally there is the evidence of superimposed footprints; these are quite common, and in all cases the later-formed print is similar in its depth and state of preservation to the earlier-formed one. These similarities are apparent even where three or more animals have trodden the same spot (see Pl. 13, Fig. C; Pl. 16, Figs B, C). Ornithopod footprints (*Wintonopus*) may be found superimposed on footprints of other ornithopods or of coelurosaurs (*Skartopus*), and the same is true for the coelurosaur footprints. Footprints of both types may be found superimposed upon those of the carnosaur. From the evidence of superimposed footprints it may be deduced (a) that the carnosaur traversed the area before some (at least) of the ornithopods and coelurosaurs did so; (b) that some ornithopods preceded some coelurosaurs; and (c) that some coelurosaurs preceded some ornithopods. But from the evidence as a whole it is possible to reach a more general conclusion: that both ornithopods and coelurosaurs traversed the Lark Quarry site at (or about) the same time, and that they did so *after* the passage of the solitary carnosaur. This is exactly the chronological sequence to be expected if the approach of the carnosaur had triggered a stampede of the ornithopods and coelurosaurs. Of course there is no absolute proof that the Lark Quarry trackways were formed in exactly this sequence, but it is difficult to imagine any other when one considers that all the ornithopod and coelurosaur track-makers were running in a single direction.

Perhaps the most striking feature of the Lark Quarry site is that all the animals responsible for *Wintonopus* and *Skartopus* trackways were headed in a single direction — about 55° E of true N, and in almost direct opposition to the course taken by the solitary carnosaur (see Pl. 4). None of these abundant ornithopod and coelurosaur trackways deviates more than a few degrees from a single compass bearing, and in this respect the Lark Quarry site appears to be unique. Dinosaur tracks uncovered at other prolific localities are randomly oriented (e.g. see de Lapparent and Montenat 1967, Tucker and Burchette 1977) or show some less obvious tendency to sub-parallel alignment (e.g. see Avnimelech 1966, Ostrom 1972). And at sites where sub-parallel trackways do predominate these often represent a 'two-way traffic' — with some trackways diametrically opposed to others (e.g. Avnimelech 1966, pl. VIII; Ostrom 1972, fig. 4). By contrast the Lark

TABLE 7: COMPARISON OF STATISTICS FOR VARIOUS TRACKWAY SITES.

site	age	area(m²)	number of footprints	number of trackways	source
Ain-Sefra, Algeria:	Triassic	1	12	?	Bassoullet 1971
St Laurent de Treves, France:	L Jurassic	25	24	?	Thaler 1962
Bendrick Rock, S Wales:	U Triassic	25	400	?	Tucker and Burchette 1977
Rocky Hill, Connecticut:	Rhaetic	930	1000+	?	Ostrom 1972
Swanage, S England:	U Jurassic	47^{e}	46	3	Charig and Newman 1962
Kerman area, Iran:	Jurassic	5	8	?6^{e}	de Lapparent and Davoudzadeh 1972
Tocantins River, Brazil:	Jurassic — Cretaceous	6–8000	47+	6	Leonardi 1980
Beth Zayit, Israel:	Cenomanian	400	200+	?10	Avnimelech 1966
F6 Ranch, Texas:	Aptian — Albian	?	76	15	Farlow 1981
Serrote do Letreiro, Brazil:	Triassic	'spacious'	?	17	Leonardi 1979
Mt Tom, Massachusetts:	Rhaetic	800	137	28+	Ostrom 1972
Lark Quarry, Queensland:	Cenomanian	209	3300+	130+	Thulborn and Wade 1979

(^{e} — estimated figures.)

Quarry trackways are more nearly parallel and (excepting the carnosaur trackway) entirely unidirectional. The coincidence of so many trackways certainly implies that some external factor controlled the behaviour of the track-makers (cf. Ostrom 1972). At the time the trackways were formed the Lark Quarry site appears to have been part of a broad drainage channel, and it is conceivable that the track-makers might have been funnelled along a common route by physical barriers such as levees or steep banks. However, there is no direct evidence of such barriers, and it may be recalled that remnants of a few randomly oriented trackways do occur at the site. These scattered and eroded remnants of trackways testify that some medium-sized bipedal dinosaurs (probably ornithopods) traversed the area before the carnosaur made its appearance, and that they did so randomly — that is, seemingly without the control of physical barriers. Apparently the behaviour of the *Wintonopus* and *Skartopus* track-makers was influenced by some factor that had not previously affected the movements of dinosaurs across the same area. Next, it is obvious that the Lark Quarry site cannot have been part of some established route along which dinosaurs were accustomed to move in either direction. Nor is it possible to believe that the dinosaurian track-makers could have adhered with absolute fidelity to a system of 'one-way' routes. One general conclusion seems inescapable: that the singular orientation of trackways at Lark Quarry must reflect some unusual behaviour on the part of the track-makers.

There can be little doubt that all the *Wintonopus* and *Skartopus* trackways at Lark Quarry were made by running animals. In most cases relative stride length is estimated to have been well over 2.9 — apparently indicative of a fast running gait equivalent to a mammalian gallop or sprint. In the few remaining cases relative stride length is estimated to have been between 2.0 and 2.9 — indicative of a gait equivalent to mammalian trotting. Our estimates of relative stride length (and hence of speed) depend in turn upon estimates of hindlimb height. The piling of estimate upon estimate may, indeed, have introduced and multiplied some errors, but these are unlikely to be of very great significance for our general conclusions. For example, in the case of the *Wintonopus* track-makers our estimates of hindlimb height are consistently greater than those that would be obtained by straightforward application of Alexander's method (1976). Consequently relative stride length (and speed) may, if anything, be underestimated for these animals. Our estimates of hindlimb height for the *Skartopus* track-makers are slightly smaller than those that would be obtained with Alexander's method; but even if our estimates are increased by as much as 40 or 50% it still appears that these dinosaurs would have been running (compare Tables 5 and 6). In any event, it is not necessary to estimate hindlimb height in order to demonstrate that the *Wintonopus* and *Skartopus* track-makers had an exceptionally long-striding gait: this is fully apparent from simple ratios of SL/FL and PL/FL (see Figs 11 and 16). Once again it appears that the Lark Quarry dinosaurs were indulging in unusual behaviour, for reports of trackways attributed to running dinosaurs are otherwise very few (see Farlow 1981, Thulborn 1982). Here it is worth recalling that the single *Wintonopus* trackway at another site (New Quarry) is that of a walking animal.

In summary, the Lark Quarry site has revealed a most unusual assemblage of dinosaur trackways, and to account for their origin it seems legitimate to postulate some exceptional pattern of behaviour on the part of the track-makers. The findings of this study seem to confirm, or even strengthen, our earlier interpretation of the trackways as evidence of a dinosaur stampede. Indeed, it is not easy to propose (let alone justify) an alternative interpretation. This difficulty arises for two reasons: (1) because all the *Wintonopus* and *Skartopus* trackways are unidirectional, and (2) because all these trackways seem to have been made by running dinosaurs. It seems very unlikely that this assemblage of trackways could represent a series of events — i.e. the passage, at intervals, of individual animals or of small groups. Any such series of events would have involved the most remarkable coincidences: at different times various dinosaurs would have traversed the same area, but always in exactly the same direction, and always at a run. Consequently one is forced to conclude that the Lark Quarry trackways represent a *single* event — a conclusion supported by the uniform preservation of the trackways. We submit that a group of more than 150 animals running in one direction must constitute a stampede or some similar event. Several experienced stockmen have examined the Lark Quarry trackways; all of them agreed that the trackways could well have resulted from a stampede, though on two occasions we were offered an alternative explanation (as a joke) — that the track-makers were being 'herded' or 'driven'.

There arise some intriguing questions. First, what caused the stampede ? Only one piece of fossil evidence seems to hint at a plausible answer — the trackway of the single carnosaur. It is quite conceivable that a gathering of ornithopods and coelurosaurs, drinking or foraging round a water-hole, might have been startled by the approach of a large predatory dinosaur. We have reservations about reading too much significance into the evidence of a single dinosaur trackway, but the only alternative is to admit that the unusual behaviour of the *Wintonopus* and *Skartopus* track-makers is inexplicable. A second question arises: why did the ornithopods and coelurosaurs run to the NE if this was the very direction from which the carnosaur had approached them? Here we can only offer speculations. The ornithopods and coelurosaurs had reached the water-hole, to the SW of the present Lark Quarry site, by some unknown and presumably preferred or 'normal' route. One might have expected these animals to have made their escape by such a route. The fact that some, at least, did not do so seems to imply that their preferred route had been blocked — perhaps by the manoeuvres of the carnosaur, which certainly made a sharp right turn. In making this turn to its right the carnosaur would simultaneously have opened up a new escape route — to the NE, and along the broad drainage channel that extended over the present Lark Quarry site towards Seymour Quarry. This reconstruction of events (Fig. 25) accords with all available evidence and seems to be fairly parsimonious. The motives of the carnosaur remain unknown; it may simply have been approaching the water-hole to drink, or it may have been hunting — perhaps attempting to corral its prey on the point extending SW into the water-hole. If the animal were hunting it is possible to speculate a little further. First, it seems likely that this large predator would have selected its prey from among the ornithopods; the coelurosaurs, insofar as they are known from their trackways, would seem to have been rather small game. Next it is conceivable that the carnosaur may not have been hunting alone: it might possibly have been assisted by another carnosaur (or perhaps even more than one) strategically placed to forestall the escaping ornithopods and coelurosaurs. This is no more than a speculation, but it might help to account for the remarkably close grouping of the ornithopods and coelurosaurs — especially since their progress over the Lark Quarry site seems not to have been constrained by physical barriers. These suggestions are not inconsistent with previous speculations on the hunting behaviour of large theropod dinosaurs (Farlow 1976).

Whatever the carnosaur's maneouvres or intentions may have been, a number of *Wintonopus* and *Skartopus* track-makers did run to the NE, across the present Lark Quarry and

Seymour Quarry sites. In doing so these animals seem to have traversed an area that they had not trodden before (or, at least, not in the immediate past). Their trackways at Lark Quarry are strictly unidirectional, and none of them seems to have been made by a walking animal. Evidently these ornithopods and coelurosaurs were not following some well-trodden path, and they may in fact have been moving across an area that was formerly unattractive to them. It is not difficult to imagine in what sense the Lark Quarry area might have been unattractive to small bipedal dinosaurs: it was covered by a layer of soft mud, into which the animals might (and certainly did) sink to a depth of several centimetres. This would have been of little consequence to a very large animal such as the carnosaur; as this animal traversed the area its feet plunged right through the mud to rest on the firmer sandy sediments below. But it is conceivable that the small coelurosaurs (mean hip height about 17 cm) and ornithopods (mean hip height about 35 cm) ran some risk of becoming bogged. If these small dinosaurs were crossing an unattractive or even dangerous area, it is reasonable to suppose that they were doing so under some quite unusual and compelling circumstances.

Our reconstruction of the events at and around Lark Quarry is illustrated in Fig. 25. This reconstruction takes into account all the peculiarities of the Lark Quarry trackways, and we have found no evidence that conflicts with it. A central assumption of this reconstruction is that the behaviour of the carnosaur was responsible, at least in some measure, for the unusual behaviour of the ornithopods and coelurosaurs. This assumption naturally implies that very little time would have elapsed between the formation of the carnosaur's trackway and the formation of the ornithopod and coelurosaur trackways. The uniform preservation of all these trackways seems to indicate that they were formed at *about* the same time ... but there is no certain way to discover if the carnosaur preceded the ornithopods and coelurosaurs by a matter of minutes or by a matter of hours. However there is one suggestive clue, provided by ornithopod and coelurosaur footprints superimposed on those of the carnosaur. In their preservation these superimposed prints are identical to those elsewhere, yet they were formed in thin streaks and pockets of mud remaining in the floor of the carnosaur's prints. The fact that these remnant patches of mud had not dried out, despite their thinness, suggests that little time elapsed (or that drying was very slow). If the intervening period were to be estimated in terms of hours, rather than minutes, we could no longer maintain our suggestion that the carnosaur's behaviour prompted the stampede of ornithopods and coelurosaurs. Even so, it would remain clear that a stampede (or some similar event) did occur — though its cause would be unknown.

The minimum distance travelled by the stampeding ornithopods and coelurosaurs is more than 95 metres — from the SW end of Lark Quarry to the NE end of Seymour Quarry. From the speed estimates presented earlier it may be calculated that most of the ornithopods and coelurosaurs covered this distance in less than 30 seconds; at their minimum speeds the slowest ornithopod and the slowest coelurosaur would have done so in 38 seconds and 45 seconds respectively. There is no indication of either the start or the end of the stampede.

Finally, it might be objected that our use of the term 'stampede' is inappropriate because the animals involved seem to have been moving at rather low speeds (mean 16 km/h for ornithopods, and mean 12 km/h for coelurosaurs). In a present-day stampede, comprising ungulate mammals, one might expect to find animals moving several times faster than the dinosaurs at Lark Quarry. However, such comparisons of absolute speeds are of limited significance — simply because the dinosaurs that traversed Lark Quarry were, on the whole, much smaller than living ungulates. To measure and compare the locomotor performances of different-sized animals it is necessary to select criteria that will reduce or eliminate the effects of size-differences. Such criteria will be examined below.

IMPLICATIONS FOR THE UNDERSTANDING OF DINOSAUR BIOLOGY

It has sometimes been supposed that juvenile dinosaurs were rare (Richmond 1965, Leonardi 1981), and that small (but adult) dinosaurs were equally rare or 'unknown' (Bakker 1972). However, there have recently been reports of juvenile dinosaurs, some no bigger than rats or pigeons, and even embryonic dinosaurs (see Bonaparte and Vince 1979, Kitching 1979, Coombs 1980a, 1982, Carpenter 1982, among others). The Lark Quarry trackways provide striking confirmation that small dinosaurs — whether adults or juveniles, or both — may have been abundant in some localities. This fact should certainly have some bearing on the debate over thermoregulation in dinosaurs, though at this point we cannot pursue so large and complicated a subject (see Thomas and Olson 1981 for a comprehensive review).

It seems impossible to distinguish with certainty between trackways made by small (but adult) dinosaurs and those made by juveniles. Consequently it is fruitless to use ichnological data in speculating about the reproductive strategies and population dynamics of dinosaurs. These aspects of dinosaur biology should more properly be investigated on the basis of body fossils — where it might prove possible to determine relationships between age, sexual maturity and body size. Nevertheless we have outlined some possibilities regarding population structure of the *Wintonopus* and *Skartopus* track-makers (Fig. 21). It must be emphasized that these are only possibilities, for we cannot agree entirely with the assumption that footprints of different sizes were made by animals of different ages (Leonardi 1981). Such an assumption is valid only if growth proceeded at a constant rate through the lives of the track-makers. Moreover the assumption would seem to be particularly suspect where there is a limited range in size of footprints (e.g. *Skartopus*, where the largest footprint is less than twice the size of the smallest). Even so, it may be legitimate to identify very small footprints as those of juveniles in cases where there is a very great range in footprint size (e.g. *Wintonopus*, where the largest footprint is nearly 12 times the size of the smallest).

Ostrom (1972) compiled data on dinosaur trackways in order to examine the possibility that some dinosaurs might have been gregarious. At various sites he found trackways grouped in near-parallel arrangement, and he concluded that several different kinds of dinosaurs may well have been gregarious in habit. Ostrom's conclusion is supported, incidentally, by the identification of dinosaurian adaptations for intra-specific combat, display and vocalization (Galton 1970, Hopson 1975, Molnar 1977, Weishampel 1981). The trackways at Lark Quarry provide strong evidence of gregarious behaviour, for they seem to have resulted (with the exception of the carnosaur trackway) from the movement of a single large group of dinosaurs. This group seems, however, to have been heterogeneous and, perhaps, rather disorganized. The trackways of coelurosaurs (*Skartopus*) and ornithopods (*Wintonopus*) are thoroughly intermingled, and there is no clear indication that the two types of dinosaur were segregated. This could indicate that these coelurosaurs and ornithopods were in the habit of moving together as a 'mixed herd', as was suggested by Krassilov (1980). In this case one might evisage the coelurosaurs as opportunists — ready to seize insects and other small animals as they were flushed from vegetation by an ornithopod herd moving through its feeding grounds. Alternatively the trackways at Lark Quarry could have resulted from accidental mingling of an ornithopod herd with one or more foraging parties of coelurosaurs. Even so it would be reasonable to regard both the ornithopods and the coelurosaurs as gregarious, for it seems unlikely that so many individuals could have gathered independently and at random in the vicinity of the Lark Quarry site. Nevertheless it is just conceivable that all the Lark Quarry track-makers were normally solitary animals: they might have been attracted to the Lark Quarry water-hole during a period of drought. However, we have found no desiccation cracks or other evidence of drought, and it may be recalled that all the trackways seem to have been formed in moist sediment. Moreover, the much-trampled claystone layer at New Quarry seems to confirm that the Lark Quarry area was quite commonly frequented by large numbers of dinosaurs.

Several studies of dinosaur trackways have employed Alexander's method (1976) to estimate the speeds of the track-makers (Russell and Béland 1976, Tucker and Burchette 1977, Coombs 1978, Thulborn and Wade 1979, Kool 1981, Farlow 1981, Thulborn 1981, 1982). These studies have made it possible to compare the speeds of various dinosaurs under various circumstances (e.g. see Russell and Béland 1976), or to compare the speeds of dinosaurs to those recorded for mammals and ground-dwelling birds (e.g. see Farlow 1981). Such comparisons of absolute speeds are certainly interesting, but they often give a poor indication of relative locomotor performances. A mammalian analogy will make this clear: if a horse, a dog and a mouse all move at 6 km/h, the horse will be walking, the dog will be trotting, and the mouse will literally be galloping (Heglund et al. 1974). Absolute speed is identical for all three animals, but their locomotor performances are obviously very different. Exactly similar relationships between size, speed and gait would have prevailed in dinosaurs, despite Kool's generalization (1981) that different-sized animals, including dinosaurs, 'all walk at roughly the same speed'

To evaluate and compare the locomotor performances of dinosaurs it is desirable to adopt some criterion that will reduce or eliminate the effect of differences in body size. In comparing the locomotor performances of fishes it is common practice to express burst speeds in terms of body lengths per second, and by analogy the speeds of dinosaurian track-makers might conveniently be expressed in terms of h /s (a 'size-related' speed, where h is height at the hip). Table 8 presents examples of such 'size-related' speeds, compared to absolute speeds, for a variety of dinosaurian track-makers. Evidently dinosaurs with similar absolute speeds may have very different 'size-related' speeds, and *vice versa.* In terms of such 'size-related' speed the locomotor performances of the Lark Quarry ornithopods and coelurosaurs are outstanding, although in terms of absolute speed these animals seem to have been moving rather slowly. However, such 'size-related' speed is no more useful for comparing locomotor performances than is absolute speed. The following (hypothetical) example, where three different-sized animals are moving at the same 'sized-related' speed, will make this clear:

h (m)	'size-related' speed (h/s)	absolute speed (m/s)	relative stride length (λ/h)	gait
0.5	3.0	1.5	1.8	walk
1.5	3.0	4.5	2.5	trot
3.0	3.0	9.0	3.1	run

Evidently the effects of size-differences are undiminished, because large animals need to attain faster gaits and higher absolute speeds in order to match the 'size-related' speeds of small animals.

Heglund, Taylor and McMahon (1974) proposed that 'speed at the trot-gallop transition point is a "physiologically similar speed" for animals of different size'. We may extend this proposition to identify two points at which animals of different sizes would attain 'physiologically similar' speeds: the walk-trot transition, and the trot-run transition. At such points different-size animals will have different absolute speeds (and different 'size-related' speeds), but their locomotor performances may be regarded as equivalent. These two points may be defined in terms of relative stride length (λ/h about 2.0 and 2.9 respectively). They may also be defined in terms of Froude number (u^2/gh; see Alexander 1976), or in terms of 'dimensionless speed' $u(gh)^{-0.5}$; see Alexander 1977). It is probably most convenient to compare locomotor performances in terms of λ/h, because estimates of this ratio have been cited in previous studies of speed in dinosaurian track-makers. From the estimates of λ/h presented here (Tables 4, 5 and 8) it is clear that the locomotor performances of the Lark Quarry ornithopods and coelurosaurs were superior (and often far superior) to those of most other dinosaurian track-makers. Estimates of Froude number and of 'dimensionless speed' (equivalent to the square root of Froude number) point to the same conclusion.

Relative stride length would seem to be a useful and fairly realistic basis on which to evaluate and compare the locomotor performances of different-size animals. But even on this basis an element of bias will emerge because there probably exists a negative correlation between body size and maximum λ/h; this seems to be the case among some living mammals (see data presented by Alexander et al. 1977), and it is reasonable to suppose that a similar relationship between size and gait prevailed among dinosaurs. Consequently straightforward comparisons of λ/h might in some cases be a little misleading; for example, two dinosaurian track-makers with λ/h estimated at 2.0 could scarcely be regarded as maintaining equivalent performances if one of them were a large dinosaur moving at maximum speed and the other were a small dinosaur capable of accelerating to greater speeds. Unfortunately there is no way to eliminate this bias, because there is insufficient evidence (either from living animals or from dinosaur trackways) to determine the regression of maximum λ/h on body size (represented by h or by body mass). All that may be said, in general terms, is that small dinosaurs probably attained higher values for maximum λ/h than did large dinosaurs. Indeed, it has been maintained (Thulborn 1982) that giant dinosaurs were unable to extend λ/h beyond 2.0 and were physically incapable of running. Nevertheless comparisons of λ/h would seem, for the present at least, to give the best indication of relative locomotor performances among dinosaurs. And on this basis the performances of the Lark Quarry ornithopods and coelurosaurs appear to be exceptional.

If the ornithopods and coelurosaurs at Lark Quarry were caught up in a stampede, or some similar event, one might expect these animals to have been running at or near their maximum speeds. And if this were the case it might be possible to determine a relationship between body size (h) and maximum running speed. Such a relationship might then be used to gain some idea of the maximum speeds of dinosaurs in general. Fig. 24A is a plot of estimated mean speed against estimated hip height for ornithopods and coelurosaurs at Lark Quarry. In this diagram it is

TABLE 8: A Comparison of the Locomotor Performances of Various Dinosaurian Track-Makers.

A. LARGE THEROPODS

ichnotaxon or track-maker	h (m)	absolute speed (m/s)	absolute speed (km/h)	relative stride length (λ/h)	size-related speed (h/s)	Froude number (u^2/gh)	dimensionless speed ($u(gh)^{-0.5}$)	source
**Megalosaurus insignis:*	1.5	2.4	8.6	1.7	1.6	0.38	0.62	de Lapparent and Zbyszewski 1957
Irenesauripus mcleani:	1.7	0.7	2.4	0.8	0.4	0.03	0.17	Sternberg 1932
**Megalosaurus:*	1.8	2.2	8.0	1.6	1.3	0.29	0.54	de Lapparent and Zbyszewski 1957
**Irenesauripus acutus:*	2.2	2.5	8.9	1.6	1.1	0.28	0.53	Sternberg 1932
**Irenesauripus occidentalis:*	2.3	0.9	3.3	0.9	0.4	0.04	0.19	Sternberg 1932
cf *Tyrannosauropus:*	2.6	1.9	6.9	1.3	0.7	0.15	0.38	this paper
**Tyrannosauropus petersoni:*	3.6	2.7	9.6	1.4	0.7	0.20	0.45	Haubold 1971

B. SMALL AND MEDIUM-SIZED THEROPODS

ichnotaxon or track-maker	h (m)	absolute speed (m/s)	absolute speed (km/h)	relative stride length (λ/h)	size-related speed (h/s)	Froude number (u^2/gh)	dimensionless speed ($u(gh)^{-0.5}$)	source
**Grallator gracilis:*	0.17	0.8	2.9	1.7	4.8	0.41	0.64	Lull 1953
**Plesiornis pilulatus:*	0.20	0.9	3.3	1.8	4.7	0.43	0.66	Lull 1953
**Grallator cursorius:*	0.32	2.4	8.7	2.3	7.5	1.86	1.36	Lull 1953
**Hopiichnus shingi:*	[a]0.55	13.1	47.2	7.0	23.8	31.99	5.66	Welles 1971
**Hopiichnus shingi:*	[b]1.00	8.2	29.5	3.8	8.2	6.86	2.62	
**Anchisauripus sillimani:*	0.69	0.5	1.9	0.9	0.8	0.04	0.20	Lull 1953
**Grallator formosus:*	0.82	1.6	5.8	1.6	2.0	0.33	0.57	Lull 1953
**Saltopoides igalensis:*	0.83	8.4	30.1	4.2	10.1	8.70	2.95	de Lapparent and Montenat 1967
**Anchisauripus exsertus:*	1.07	2.1	7.7	1.8	2.0	0.43	0.66	Lull 1953
**Dilophosauripus williamsi:*	1.37	1.3	4.8	1.3	1.0	0.13	0.37	Welles 1971
**Ornithomimipus angustus:*	1.56	1.3	4.8	1.2	0.9	0.12	0.34	Sternberg 1926
[c]Theropod Q94/98:	1.16	12.1	43.6	4.9	10.4	12.94	3.60	Farlow 1981
	1.46	10.1	36.4	3.9	6.9	7.16	2.68	
[c]Theropod BLV/A3:	1.48	9.4	33.8	3.7	6.4	6.12	2.47	Farlow 1981
	1.85	7.9	28.3	3.0	4.3	3.42	1.85	
[c]Theropod 86/0–82:	1.52	11.9	42.8	4.3	7.8	9.55	3.09	Farlow 1981
	1.90	10.0	35.9	3.5	5.4	5.34	2.31	
Skartopus Nr 25:	0.18	2.2	8.0	2.7	12.1	2.73	1.65	this paper[d]
Skartopus (mean):	0.17	3.2	11.6	3.7	18.8	6.18	2.49	
Skartopus Nr 2:	0.13	4.4	15.9	4.9	33.1	14.92	3.86	

C. ORNITHOPODS

ichnotaxon or track-maker	h (m)	absolute speed (m/s)	absolute speed (km/h)	relative stride length (λ/h)	size-related speed (h/s)	Froude number (u^2/gh)	dimensionless speed ($u(gh)^{-0.5}$)	source
**Anomoepus minimus:*	0.28	0.3	1.2	0.9	1.2	0.04	0.20	Lull 1953
Amblydactylus kortmeyeri:	0.64	0.8	2.8	1.1	1.2	0.10	0.31	Currie and Sarjeant 1979

**Anomoepus crassus:*	0.84	0.6	2.3	0.9	0.7	0.05	0.22	Lull 1953
**Sauropus barrattii:*	0.88	1.9	6.7	1.7	2.1	0.40	0.63	Lull 1953
Irenichnites gracilis:	0.89	1.6	5.9	1.6	1.9	0.31	0.56	Sternberg 1932
**Satapliasaurus dsocenidzei:*	1.08	1.0	3.5	1.1	0.9	0.08	0.30	Gabouniya 1951
**Gypsichnites pacensis:*	1.74	1.3	4.8	1.2	0.8	0.10	0.32	Sternberg 1932
[e]Ornithopod:	3.44	7.6	27.2	2.7	2.2	1.70	1.30	Brown 1938
	3.44	2.4	8.6	1.3	0.7	0.17	0.41	
Wintonopus Nr 44:	0.42	2.5	9.2	2.2	6.0	1.53	1.24	
Wintonopus (mean):	0.35	4.6	16.5	3.7	13.3	6.26	2.50	this paper[d]
Wintonopus Nr 21:	0.29	6.3	22.7	5.0	21.7	14.03	3.75	
Wintonopus (New Quarry):	0.47	1.1	4.0	1.5	2.3	0.26	0.51	this paper

In most cases h is estimated by methods introduced in this paper.

*stride length estimated from published data (e.g. pace length or ratio of pace length: footprint length).

[a] with h estimated as for an ornithomimid; equation (14).

[b] with h estimated by Welles (1971).

[c] first estimate of h represents four times footprint length, after Farlow (1981); second estimate is the mean of two, calculated as for a carnosaur and as for a coelurosaur (equations (7) and (12) respectively).

[d] all track-makers at Lark Quarry. First estimate represents the worst-performing track-maker (in terms of λ/h), and the third estimate represents the best-performing track-maker. Track-makers are listed by number in Tables 4 (*Wintonopus*) and 5 (*Skartopus*).

[e] two interpretations of single trackway (Russell and Béland 1976; Thulborn 1981), both with h estimated as four times footprint length.

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immediately obvious that the trend (or first principal axis) of the distribution is roughly parallel to the regression lines defining size/speed relationships at the walk-trot transition (λ/h 2.0) and the trot-run transition (λ/h 2.9). This parallelism is not an artefact generated by our methods for estimating size and speed (note size/speed relationship for the New Quarry ornithopod); nor does it appear to be fortuitous. Instead it demonstrates very clearly that most animals at Lark Quarry were running and, moreover, that animals of different sizes were maintaining equivalent locomotor performances (in terms of λ/h). Mean λ/h for the ornithopod track-makers is estimated to be 3.69; for the coelurosaur track-makers it is estimated to be 3.71. Fig. 24B is similar to Fig. 24A, except that it illustrates the relationship between estimated *maximum* speed and estimated hip height. In this diagram the line drawn through the distribution is not derived from our data: it is a line defining the *theoretical* regression of speed on size (h) when λ/h is at a value of 3.93. (The figure of 3.93 was selected on the basis of our findings: among the ornithopod track-makers the mean figure for maximum λ/h per trackway is 3.94, and among the coelurosaurs it is 3.92). Evidently the actual relationship between size and speed conforms quite closely to the theoretical relationship at this particular value for λ/h. In other words most of the Lark Quarry track-makers seem to have been running at a 'physiologically similar [or standard] speed' — even though the track-makers were of various sizes and had different absolute speeds. It seems quite probable that the 'physiologically similar' speed shared by the Lark Quarry dinosaurs did represent maximum or near-maximum speed. If this were not so one might reasonably expect that small animals would have matched the absolute speeds of larger ones. Further, it is difficult to conceive of any circumstances that might have led different-sized dinosaurs to run at a 'physiologically similar' speed less than maximum speed. From the evidence presented in Fig. 24 we may deduce that small bipedal dinosaurs, with h up to about 60 cm, could attain maximum λ/h of at least 3.93. In our preliminary account of the Lark Quarry site (Thulborn and Wade 1979) we attempted to account for the 'rather low' absolute speeds of the track-makers by suggesting that the animals might have been fatigued, or that they might have been retarded by sinking deeply into the muddy substrate. However, we have found no evidence that the track-makers were decelerating to any marked degree, and Alexander pointed out (1976) that relationships between body size, speed and stride length did not seem to be seriously affected by the consistency of the substrate. Even so, it may be more accurate to re-phrase our general conclusion as follows: that the Lark Quarry animals were running at maximum or near-maximum speed *under the conditions that then prevailed.* We cannot determine to what extent those prevailing conditions might have affected the locomotor performances of the Lark Quarry dinosaurs.

If small bipedal dinosaurs were capable of attaining maximum λ/h about 3.93 we may estimate the maximum speeds of these animals by substituting $3.93h$ for λ in equation (*2*). This equation may then be re-written as follows:

$$(15) \qquad u \cong [gh\,(3.93h/1.8h)^{2.564}]^{0.5}$$

and simplied to give:

$$(16) \qquad u \cong (72.22h)^{0.5}$$

where h is in metres and u is solved in metres per second. This equation may be applied equally well to trackway data (with h estimated from footprint dimensions) or to osteometric data (with h measured directly). The maximum estimate of λ/h for any of the Lark Quarry track-makers is 5.03 (for a *Wintonopus* track-maker, No. 21 in Table 4). If this figure (rather than 3.93) represents maximum λ/h for small bipedal dinosaurs we may estimate their maximum speeds by substituting it for λ in equation (*2*). The equation may then be re-written and simplified to give:

$$(17) \qquad u \cong (136h)^{0.5}$$

However, the assumption behind this equation is that nearly all track-makers at Lark Quarry would have been running at somewhat less than their maximum possible speeds. Consequently it seems reasonable to qualify our conclusions as follows: the Lark Quarry track-makers seem to have attained maximum λ/h of at least 3.93 and, in some instances, as high as 5.03. If these conclusions do have more general application it should be possible to predict maximum running speed for any small bipedal dinosaur ($h < 70$ cm) that is known from a skeleton or a trackway: its maximum speed would probably lie between the two estimates to be obtained with equations (*16*) and (*17*). It might also be legitimate to make use of these equations in estimating maximum speeds for some medium-size bipedal dinosaurs (with h up to 1.5 or 2 m), but it is certainly not appropriate to do so for very large bipeds or quadrupeds. This is because a dinosaur moving with λ/h as high as 3.93 must incorporate an unsupported interval in each stride, and the ability to use unsupported intervals is generally restricted to animals with body mass less than 500–800 kg (see discussions by Coombs 1978, Thulborn 1982). Many large bipedal dinosaurs were certainly above this critical weight limit, as were nearly all of the quadrupedal forms (see, for example, the body weights estimated for dinosaurs by Colbert 1962). Coombs indicated (1978) that the best mammalian runners had optimum body mass of about 50 kg — but not over 500 kg or below 5 kg — and it seems likely that dinosaurs would have been under similar physical constraints. In addition it is possible that the maximum speeds of quadrupedal dinosaurs were restricted by structural peculiarities of the limbs and their girdles (see Thulborn 1982). Even so, it may be legitimate to apply equations (*16*) and (*17*) in the case of some quite large bipedal dinosaurs that seem to have been very lightly constructed. Notable among these are the ornithomimids or 'ostrich dinosaurs'; these animals possess striking cursorial adaptations and are commonly supposed to have been the swiftest of all dinosaurs (Russell 1972, Coombs 1978). One example of the ornithomimid *Dromiceiomimus* has skeletal hip height of 1.22 metres and is estimated to have had a live body weight of about 154 kg (Russell and Béland 1976); with equation (*16*) the maximum speed of this animal may be estimated at 9.31 m/s (33.5 km/h). Among the ornithomimids described by Osmólska et al. (1972) the largest example (*Gallimimus*) has skeletal hip height of 1.94 metres; this dinosaur's maximum speed may be estimated at 11.82 m/s (42.6 km/h). These speeds (c. 35–45 km/h) could conceivably be the highest attained by any of the dinosaurs. However, it is certainly possible that the ornithomimids were able to extend relative stride length beyond 3.93 — particularly in view of their cursorial adaptations. Russell and Béland (1976) used Alexander's method (1976) to consider the hypothetical example of an ornithomimid (h about 1.22 metres) running at 80 km/h; at this speed the animal's stride length would have been about 8.6 metres, indicating λ/h about 7.05. It is difficult to imagine that any dinosaur could have extended stride length to such a degree. Among living mammals such a high figure for λ/h is achieved only by the most highly adapted of quadrupeds — which are able to employ stride-lengthening techniques unavailable to bipeds (e.g. scapular rotation and flexion/extension of the vertebral column). An example may help to make this clear. At a speed of 10 m/s (36 km/h) a human sprinter with hip height about 95 cm will have relative stride length in the region of 4.6 — as estimated with equation (*2*). To attain λ/h of 7.0 a human athlete .must perform a leap. We suspect that similar constraints apply to ratites, though we have been unable to find suitable data on these animals. By comparison it is unlikely that a bipedal dinosaur could have maintained a running gait with λ/h as high as 7.05, even though the ornithomimids may have reached maximum values of λ/h somewhat higher than 3.93. If the largest ornithomimid mentioned above (*Gallimimus,* with h of 1.94 metres) had been capable of achieving maxmium λ/h of 5.0 its maximum speed would have been about 16 m/s (58 km/h) — as estimated by means of equation (*17*).

The general conclusion to be drawn from the Lark Quarry trackways is that small bipedal dinosaurs ($h < 70$ cm) attained maximum λ/h of at least 3.93, and possibly as high as 5.03. These same figures for maximum λ/h might also apply to somewhat larger bipedal dinosaurs, providing that these had live body weights less than 500–800 kg. Larger and heavier dinosaurs, both bipeds and quadrupeds, probably attained lower figures for maximum λ/h — simply because they would have been too heavy to have made use of unsupported intervals. If the most highly adapted of dinosaurian cursors — the ornithomimids — did have maximum λ/h of about 3.93 their maximum speeds might have been about 35–45 km/h. Even if ornithomimids were capable of attaining λ/h as high as 5.03 their maximum speeds might still have been no greater than about 60 km/h. These estimates fall rather short of the maximum possible speeds attributed to ornithomimids on the basis of anatomical comparisons (70–80 km/h, or even more; see Russell 1972).

Are these general conclusions supported or contradicted by evidence from other dinosaur trackways? Trackways attributed to running dinosaurs appear to be uncommon, but we will examine those few examples that have come to our attention. In describing a short section of ornithopod trackway from the Cretaceous of Colorado, Brown (1938) mentioned that each footprint measured 34 inches (c. 86 cm) in width and length, and that the track-maker had 'stepped' a distance of 15 feet (c. 4.6 metres). Brown did not suggest that this trackway had been made by a running dinosaur: instead he accounted for the remarkably long stride by suggesting that the track-maker was a gigantic creature nearly twice the height of *Tyrannosaurus* in its classic standing pose (i.e. 35 feet as opposed to 18 feet). By using Alexander's methods (1976) to determine speed and hip height Russell and Béland (1976) estimated that this trackway had been made by a very large animal (h about 3.44 metres) running at a speed of 7.54 m/s (27.1 km/h). Russell and Béland estimated that the Colorado ornithopod had weighed about 11 tonnes, and from their figures it may be calculated that λ/h was in the region of 2.7. These estimates have, at best, an indirect bearing on our general conclusions: if a giant dinosaur was capable of running at 27 km/h one might reasonably expect the much smaller dinosaurs at Lark Quarry to have matched, or even surpassed, such a speed. However, it may be recalled that the best available measure for comparing locomotor performances seems to be relative stride length (λ/h), rather than absolute speed. Moreover there is a suspicion that Brown may have misinterpreted the Colorado trackway, and that the dinosaur responsible for it was actually walking (λ/h 1.34) at a speed no greater than 8.5 km/h (see Thulborn 1981).

In *Saltopoides igalensis,* the trackway of a bipedal dinosaur from the Rhaeto-Liassic of France, de Lapparent and Montenat (1967) found the ratio PL/FL to be as high as 11/1 (see Fig. 16). These authors considered that the track-maker was most probably a long-legged coelurosaur; they gave a figure of 15.5 cm for footprint length, and from their diagram of the trackway (1967, fig. 15B) we estimate stride length to have been about 344 cm. The *Saltopoides* footprints are rather large by coelurosaurian standards (see Table 2), and they could quite possibly have been made by a medium-size theropod closer in appearance to carnosaurs. Alternatively the track-maker might have been a rather large coelurosaur with 'typical' hindlimb proportions, or a coelurosaur with hindlimb proportions resembling those of ornithomimids. By considering all these possibilities we may obtain several estimates of size and speed for the track-maker:

assumed status of track-maker	h (m)	λ/h	*estimated speed* (m/s)	(km/h	*equations used* (h)	(speed)
'typical' coelurosaur	0.70	4.9	9.45	34.0	*(12)*	*(11)*
carnosaur-like	0.93	3.7	7.57	27.3	*(7)*	*(11)*
ornithomimid-like	0.85	4.0	8.10	29.2	*(14)*	*(11)*

In each case λ/h is found to be greater than 2.0, so that speed is most appropriately estimated with equation (*11*). These estimates of speed and relative stride length are in fair agreement with the conclusions we have drawn from the Lark Quarry trackways, and they might be taken to indicate that the *Saltopoides* track-maker was running at or near its maximum speed. It is noteworthy that all three estimates of λ/h are below 5.0.

From the Kayenta Formation of Arizona (Early Jurassic or Late Triassic) came a sequence of three dinosaur footprints described by Welles (1971) as *Hopiichnus shingi*. The maker of this trackway was evidently a long-striding bipedal dinosaur: footprint length was about 10 cm whereas pace length was found to be 191 cm. Welles commented that pace length was 'tremendous' in relation to the size of the footprints (compare data in Fig. 16), but he did not suggest that the track-maker had been running. He considered, instead, that the track-maker had been an exceptionally long-limbed animal (perhaps an ornithomimid) with h about 1 metre. Dr Welles also informs us (pers. comm.) that the morphology of the footprints seems to indicate a walking gait rather than a running gait. We may consider several estimates of size and speed for the *Hopiichnus* track-maker:

assumed status of track-maker	h (m)	λ/h	*estimated speed*		*equations used*	
			(m/s)	(km/h)	(h)	(speed)
'typical' coelurosaur	0.42	9.0	16.03	57.7	(*12*)	(*11*)
ornithomimid-like	0.55	7.0	13.10	47.2	(*14*)	(*11*)
ornithomimid-like	1.00	3.8	8.18	29.5	–	(*11*)
ornithomimid-like	1.00	3.8	7.32	26.4	–	(*6*)

In the last two cases h is the estimate by Welles (1971); and in one of these speed is estimated by means of equation (*6*), which is appropriate for walking animals, even though λ/h is greater than 2.0. It seems impossible to draw any firm conclusions from these estimates of size, speed and relative stride length. For the animal to have been walking (with λ/h less than 2.0) it would need to have been at least 1.9 metres high at the hip; this improbably high figure is equivalent to 19 times footprint length. It may be recalled that Alexander (1976) found h to be approximately 4 times footprint length among bipedal dinosaurs; and even on the assumption that the track-maker could have been an ornithomimid-like dinosaur we estimate h to have been less than 6 times footprint length (see the second of the cases listed above). If we adopt Welles's estimate for h (equivalent to 10 times footprint length) the *Hopiichnus* track-maker is found to be similar to the Lark Quarry track-makers in terms of size/speed relationship (λ/h 3.82 as opposed to mean of 3.93). This close correspondence in relative stride length might indicate that the *Hopiichnus* track-maker was running at or near its maximum speed — if it were indeed an extremely long-limbed dinosaur. Estimates of h obtained with equations (*12*) and (*14*) are equivalent to 4.2 and 5.5 times footprint length (see the first two cases listed above), but these indicate that λ/h was as high as 7.0 or 9.0. It is difficult to imagine that any bipedal dinosaur could have attained such values for relative stride length. In summary, we are unable to offer any satisfactory interpretation of the *Hopiichnus* trackway. If the track-maker had hindlimb proportions resembling those in any known dinosaur it must have been progressing in a series of phenomenal leaps. If the track-maker had been using a running gait (λ/h from 2.9 up to about 5.0) it must have had hindlimbs about twice as long as those of an ornithomimid with comparable foot length. And if the track-maker had been walking (λ/h less than 2.0) it must have had hindlimbs about 3 times as long as those of an ornithomimid with comparable foot length. There is no indication that the animal might have been swimming, and only touching down occasionally with its feet (cf. theropod trackways described by Coombs 1980b).

Alexander's methods (1976) have recently been applied by Farlow (1981) to a series of 15 dinosaur trackways in the Cretaceous of Texas. Three of these trackways seem to have been made by fast-running animals, with λ/h in the range 3.7 to 4.9 and speeds estimated from 30 to 43 km/h. Once again it is noteworthy that estimates of λ/h are less than 5.0. Farlow identified the Texas track-makers as theropod dinosaurs, and from the size of their footprints they might be envisaged either as exceptionally large coelurosaurs or as small to medium-size carnosaurs. Consequently it is possible to compare several estimates of size and speed for these track-makers:

assumed status of track-maker	*h* (m)	λ/h	*estimated speed* (m/s)	(km/h)	*equations used* (*h*)	(speed)
*Q94/98:						
theropod	1.16	*4.9	*11.9	*42.8	–	*(6)*
theropod	1.16	*4.9	*12.1	43.6	–	*(11)*
coelurosaur-like	1.42	4.0	10.3	37.0	*(12)*	*(11)*
carnosaur-like	1.49	3.8	9.9	35.7	*(7)*	*(11)*
*BLV/A3:						
theropod	1.48	*3.7	*8.3	*29.9	–	*(6)*
theropod	1.48	*3.7	*9.4	33.8	–	*(11)*
coelurosaur-like	1.87	2.9	7.7	28.0	*(12)*	*(11)*
carnosaur-like	1.82	3.0	8.0	28.6	*(7)*	*(11)*
*86/0-82:						
theropod	1.52	*4.3	*11.1	*39.9	–	*(6)*
theropod	1.52	*4.3	*11.9	42.8	–	*(11)*
coelurosaur-like	1.93	3.4	9.8	35.4	*(12)*	*(11)*
carnosaur-like	1.86	3.5	10.1	36.4	*(7)*	*(11)*

(*trackway identification numbers and estimates taken from Farlow, 1981)

None of these estimates seems to be in serious conflict with our general conclusions. If h is estimated as 4 times footprint length only one of the track-makers (Q94/98) is found to have attained λ/h very much greater than 3.93. If h is estimated with the methods introduced in this paper it appears that this same track-maker would have rivalled the Lark Quarry dinosaurs in its locomotor performance (λ/h 3.8 to 4.0).

To summarize, we have found no certain evidence that any bipedal dinosaur greatly surpassed the locomotor performances of the Lark Quarry dinosaurs. The Colorado ornithopod (Brown 1938) may have been walking with λ/h about 1.34 (Thulborn 1981); even if the track-maker had been trotting or running (Russell and Béland 1976) λ/h would have been no greater than 2.7. The *Saltopoides* track-maker (de Lapparent and Montenat 1967) seems certainly to have been running, with mean λ/h of 4.2 (based on three estimates for h). If this track-maker had resembled carnosaurs or ornithomimids in body build it would appear to have matched the locomotor performances of the Lark Quarry animals, having λ/h in the range 3.7 to 4.0. But if the *Saltopoides* track-maker is envisaged as an exceptionally large coelurosaur with 'typical' hindlimb proportions its locomotor performance (λ/h 4.9) is matched by only a few of the Lark Quarry dinosaurs. The *Hopiichnus* trackway (Welles 1971) presents intractable problems of interpretation. If this track-maker resembled any known dinosaur in hindlimb proportions its locomotor performance must have been phenomenal: λ/h would have been at least 7.0, and possibly 9.0 or higher. It is difficult to believe that any bipedal animal could sustain a running gait with such figures for λ/h. But if the *Hopiichnus* track-maker had achieved this feat it would be necessary to abandon, or at least modify, the conclusions we have drawn from the Lark Quarry trackways. In this case further problems would arise. If the *Hopiichnus* track-maker *and* the Lark Quarry track-makers were running at or near maximum speed we might be forced to question Alexander's findings (1976, 1977) on the relationships of size, speed and gait in living tetrapods. Alternatively we must suppose that the Lark Quarry dinosaurs were very severely retarded by sinking into the muddy substrate (with the effect of reducing λ/h from at least 7.0 to 4.0 or less). If the Lark Quarry track-makers had been running well below their maximum possible speeds (but were not seriously retarded by the muddy substrate) another question will emerge: what circumstances caused these animals to run at a 'physiologically similar speed' ($\lambda/h \cong 3.93$) a good deal less than maximum speed? We cannot find a satisfactory answer. Next it might be surmised that the *Hopiichnus* track-maker had been travelling with λ/h no greater than 5.0 (the maximum estimate from any trackway considered here); in this case the track-maker must be envisaged as an animal with hindlimbs very much longer (relative to foot length) than those in any known dinosaur. Evidently all these interpretations of the *Hopiichnus* trackway present difficulties; for the present we must regard the significance of this trackway as uncertain or equivocal. Finally we estimate that the three fastest of the Texas theropods (Farlow 1981) were travelling with λ/h between 2.9 and 4.0. These theropods, whether coelurosaurs or carnosaurs, seem to have maintained locomotor performances equivalent or inferior to those of the Lark Quarry dinosaurs.

CONCLUSIONS

The most reliable guide to the size of a dinosaurian track-maker is probably footprint size index (SI) — rather than footprint length (FL) or any similar dimension. This conclusion is based on analysis of variance in a sample of 57 *Wintonopus* trackways, and it remains to be tested elsewhere. The *Skartopus* trackways cannot be used to test this conclusion because they do not show sufficient variation in size.

In bipedal dinosaurs the anatomy and posture of the foot were such that metatarsus length (MT) can be estimated on the basis of footprint dimensions (Fig. 18). Such an estimate of MT can then be used to predict skeletal hip height (h) because these two dimensions are strongly correlated in each major group of bipedal dinosaurs. We provide allometric equations to predict h in the following groups of dinosaurs: coelurosaurs (with 'typical' hindlimb proportions), ornithomimids, carnosaurs, ornithopods in general, cursorial ornithopods, and graviportal ornithopods. These equations were used to obtain the following estimates of h for dinosaurian track-makers at the Lark Quarry site: about 2.6 m for the single carnosaur (trackway identified as cf. *Tyrannosauropus*); from 14 cm to 70 cm for the numerous ornithopods (trackways identified as *Wintonopus latomorum* ichnogen. et ichnosp. nov.), but with one large individual at about 1.6 m; from 13 to 22 cm for the numerous coelurosaurs (trackways identified as *Skartopus australis* ichnogen. et ichnosp. nov.).

The carnosaur traversed the Lark Quarry area from NE to SW, and a mixed group of ornithopods and coelurosaurs subsequently crossed the same area in the opposite direction. This mixed group comprised at least 150 animals. The gaits of these (and other) dinosaurian track-makers must be defined arbitrarily: this is because bipedal dinosaurs had the same sequence of limb movements at all speeds (and because the sequence of limb movements is unknown in quadrupedal dinosaurs). We define three dinosaurian gaits on the basis of relative stride length (λ/h): a walking gait ($\lambda/h < 2.0$), a trotting gait (λ/h between 2.0 and 2.9), and a running gait ($\lambda/h > 2.9$). These may be regarded as 'physiologically similar' to the walking, trotting and running gaits of mammals (see Heglund et al. 1974, Alexander 1977). On this basis it is determined that the carnosaurian track-maker was walking (λ/h 1.3) whereas the ornithopods and coelurosaurs were using a fast running gait equivalent to cantering or galloping in mammals (mean λ/h about 3.7). An ornithopod track-maker at a second site (New Quarry) was found to have been walking (λ/h 1.5).

The relationships between size (h), speed and gait in living tetrapods (see Alexander 1976, 1977; Alexander et al. 1977) were used to estimate the speeds of the track-makers. It is estimated that the carnosaur was walking at a speed of about 7 km/h; for a sample of 56 ornithopods mean speed is estimated to have been about 16 km/h, and for a sample of 34 coelurosaurs it is estimated to have been about 12 km/h. For the single ornithopod at New Quarry estimated speed is 4 km/h.

The findings of this study support our preliminary interpretation of the Lark Quarry trackways — that the ornithopods and coelurosaurs were caught up in a stampede, which may have been generated by the approach of the carnosaur (Thulborn and Wade 1979, Wade 1979). We can find no evidence that conflicts with this interpretation. Indeed, it is difficult to imagine any other circumstances that might account for a mixed group of 150 dinosaurs running in a single direction. Moreover there is some indication that the ornithopods and coelurosaurs were running at or near their maximum speeds (under the conditions that prevailed): different-sized individuals were moving at different absolute speeds, but they seem to have maintained a 'physiologically similar speed' measured in terms of relative stride length ($\lambda/h \cong 3.7$). It is difficult to believe that so many animals could have maintained and shared a 'physiologically similar speed' other than maximum speed.

To measure and compare the locomotor performances of dinosaurian track-makers it is desirable to adopt some criterion that will eliminate (or at least reduce) the effects of differences in body size. Direct comparisons of absolute speed are of little value because they are biased in favour of larger animals; comparisons of a 'size-related' speed (h/s, analogous to body lengths per second in studies of fish locomotion) are equally biased in favour of small animals. Of the criteria that are available for appraising locomotor performance the most suitable would seem to be relative stride length (λ/h), Froude number (see Alexander 1976), and 'dimensionless speed' (see Alexander 1977). In terms of these criteria the locomotor performances of the Lark Quarry ornithopods and coelurosaurs are outstandingly good; their performances are better (and usually far better) than those of most other dinosaurian track-makers.

The ornithopods and coelurosaurs at Lark Quarry attained maximum λ/h of at least 3.9, and possibly as high as 5.0. This latter figure might represent the maximum limit of relative stride length for any bipedal dinosaur: it is difficult to imagine that any bipedal animal could extend λ/h much beyond 5.0, and we have found no certain evidence of any dinosaur having done so. If the most highly adapted of dinosaurian cursors — the ornithomimids — attained λ/h of 5.0 their maximum speeds might have been about 60 km/h.

Finally it is clear that small dinosaurs, whether juveniles or adults (or both), may have been abundant in some localities. It may not be legitimate to identify small footprints as those of juvenile dinosaurs, because dinosaurian rates of growth are unknown and may not have been constant. For this reason it is probably fruitless to investigate dinosaurian demography on the basis of ichnological data.

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In June 1982 Lark Quarry and a surrounding area (about 374 hectares) were designated an Environmental Park under the joint trusteeship of the Winton Shire Council and the Queensland Museum. This end was achieved through the goodwill and co-operation of Roslyn and Bob Blackett ('Amelia Downs'), members of the Winton Shire Council, and officers of the Queensland National Parks and Wildlife Service (especially Alan Chenoweth and Warren Oxnam). The Winton Shire Council has constructed an access road to the trackway site, which is now furnished with a permanent walkway and a protective roof (designed by Duncan McPhee, who also worked on site during excavations). Neville Agnew (Conservator, Queensland Museum) is undertaking a long-term study to monitor and retard any deterioration of the trackway surface.

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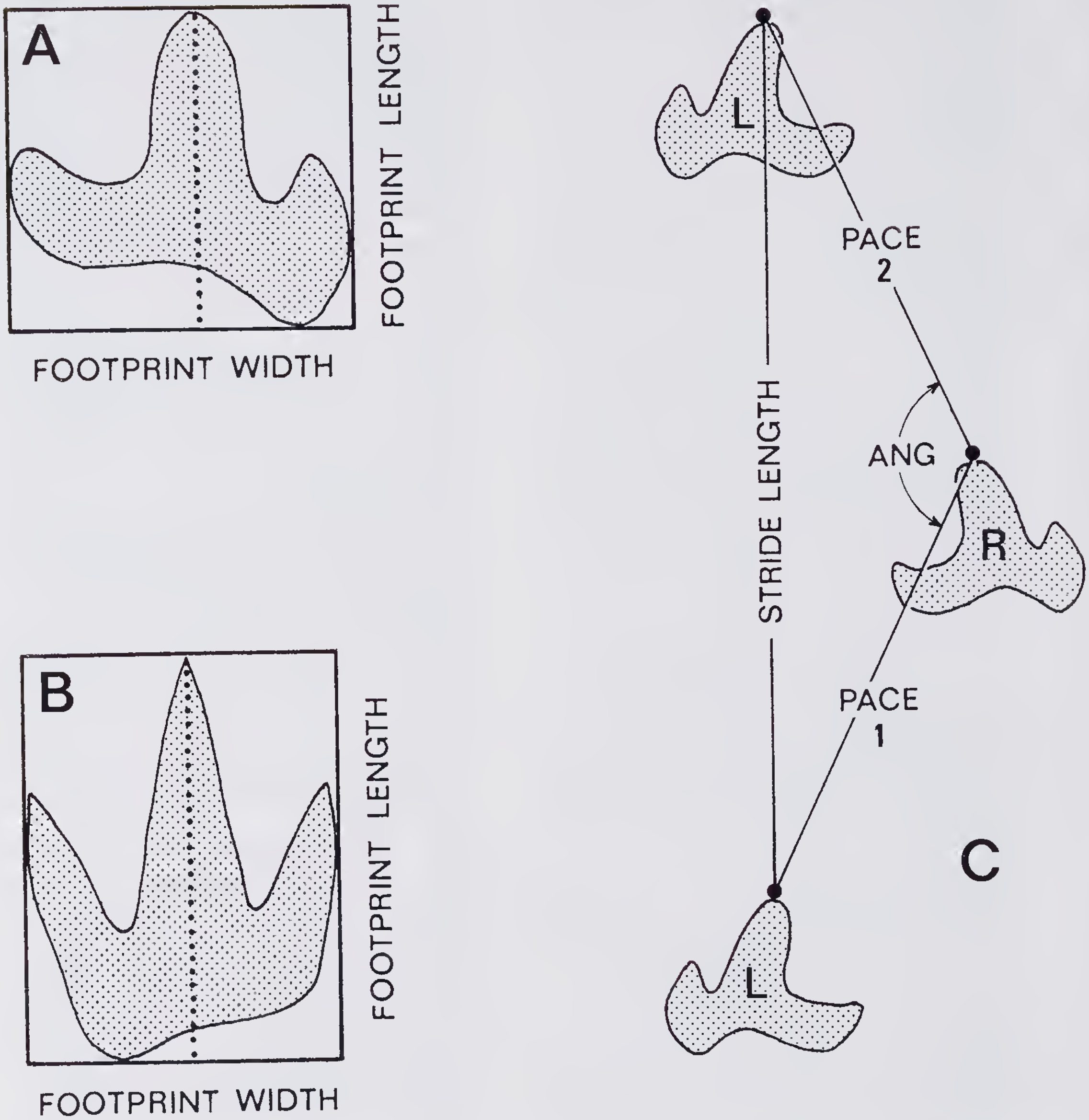


FIGURE 2. Diagrams to illustrate measurements of footprints and trackways. A, outline of ornithopod footprint showing footprint length measured along or parallel to the axis of digit 3 (dotted line); footprint width is measured at a right angle to footprint length. B, outline of coelurosaur footprint showing corresponding measurements of length and width. C, short section of ornithopod trackway showing measurements of two successive paces and a single stride. Pace angulation (ANG) is calculated from the lengths of the paces and the stride (see 'Methods').

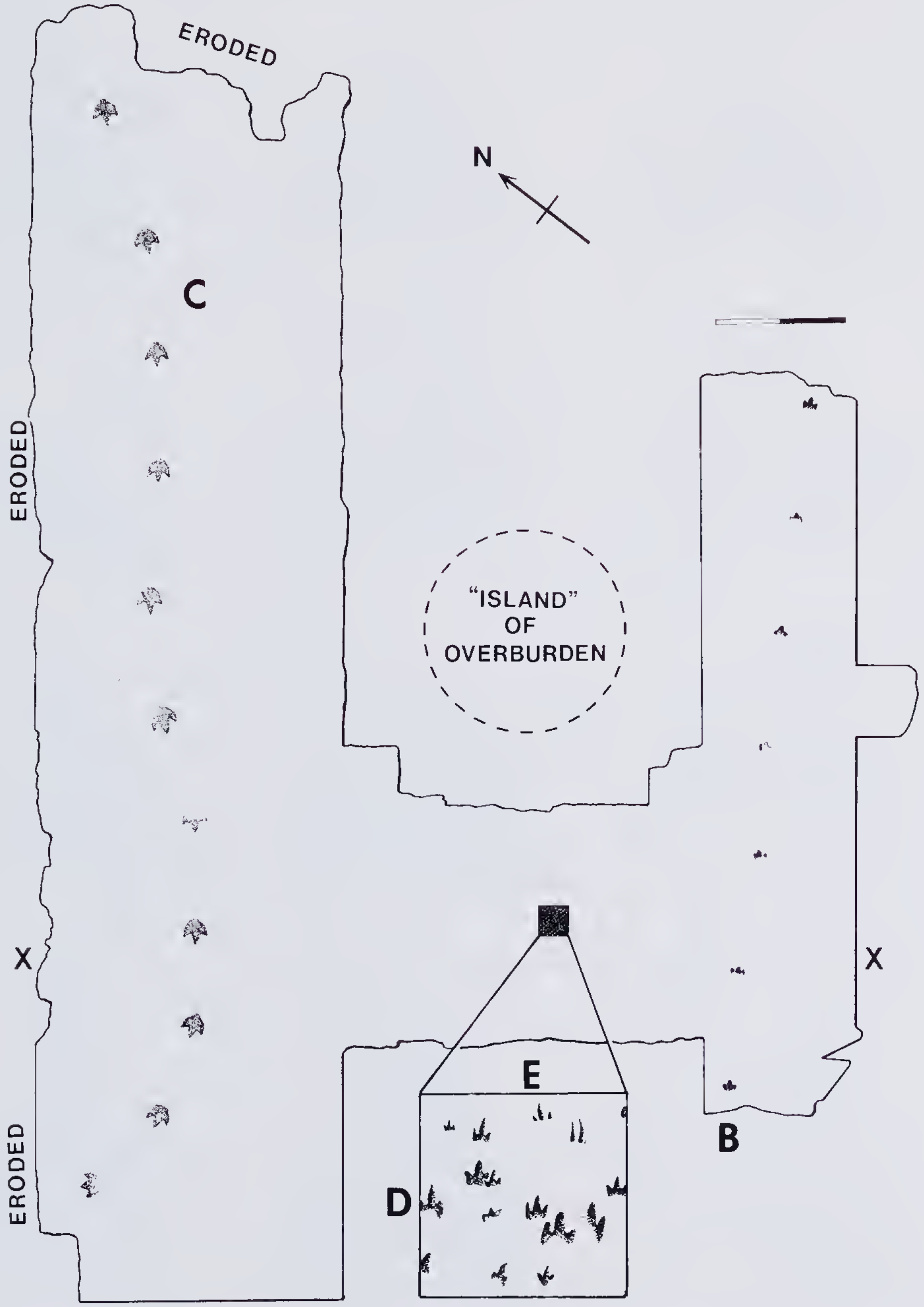


FIGURE 3. Outline chart of the study area at Lark Quarry. Scale bar indicates 2 m. Trackway of the solitary carnosaur is shown at left (C), and partly eroded trackway of an exceptionally large ornithopod is shown at right (B). A representative portion of the bedding plane is enlarged (bottom centre) to illustrate the abundance and orientation of small footprints attributed to ornithopods (D) and coelurosaurs (E). Trackways are identified by corresponding letters in descriptions (p. 417). The number of track-makers was estimated by counting footprints in a metre-wide transect between the points marked X. The area shown in outline was photographed (see Pl. 4), replicated in fibreglass and studied in detail. Adjoining areas of bedding plane (mainly to S and SW) were exposed during excavations but were not studied in detail. An outlier or 'island' of overburden was left undisturbed in the area indicated.

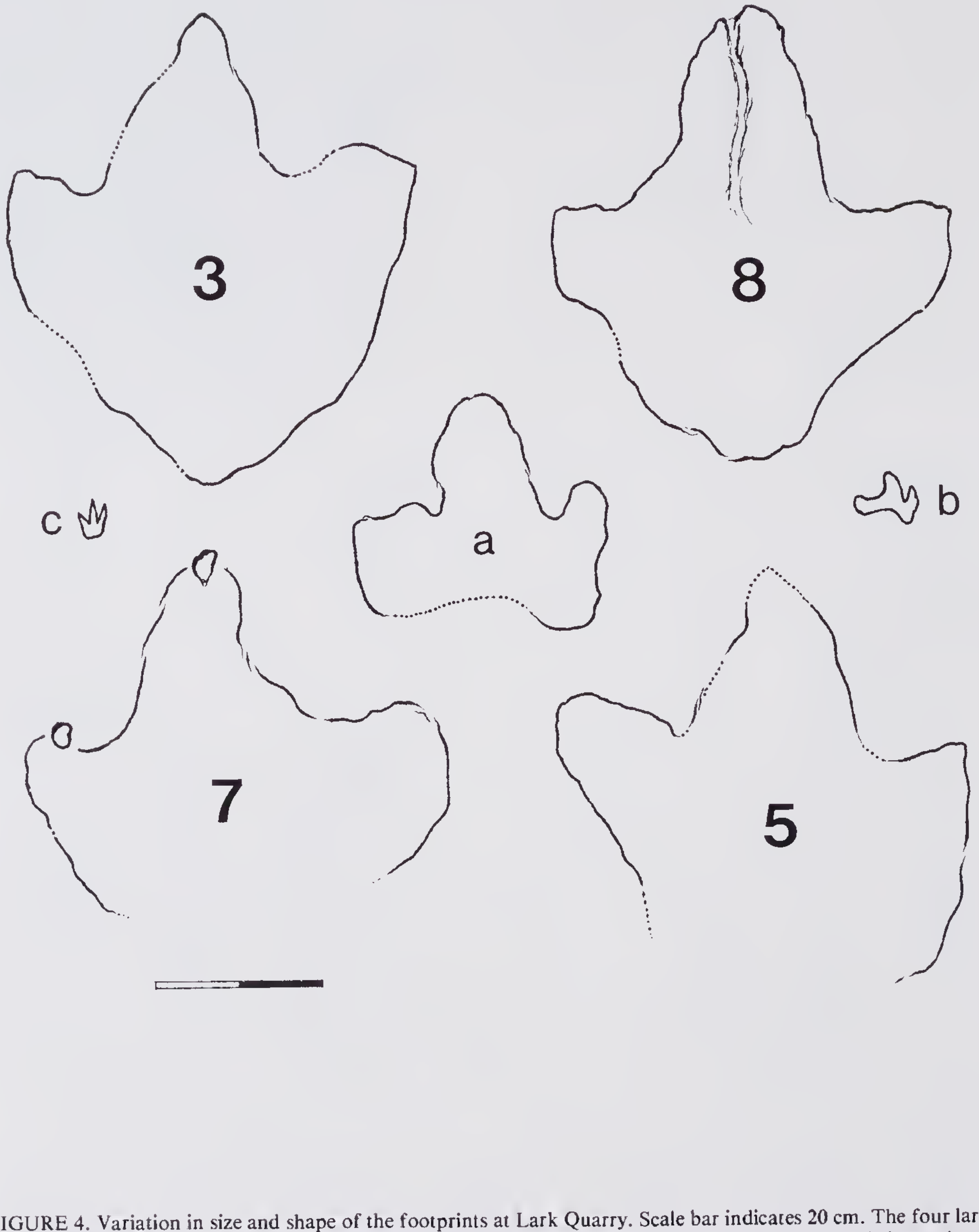


FIGURE 4. Variation in size and shape of the footprints at Lark Quarry. Scale bar indicates 20 cm. The four large footprints are from the trackway of the carnosaur (cf. *Tyrannosauropus*) and are identified by their number in the sequence 1–11. Footprint 7 shows traces of large pointed claws (see also Pl. 6); footprint 8 shows a longitudinal crest formed by mud adhering to the underside of the track-maker's middle toe. *a*, the largest ornithopod footprint (*Wintonopus*) found at Lark Quarry. *b*, an 'average' ornithopod footprint (*Wintonopus*) at Lark Quarry, based on mean dimensions in 284 examples. *c*, an 'average' coelurosaur footprint (*Skartopus*) at Lark Quarry, based on mean dimensions in 191 examples.

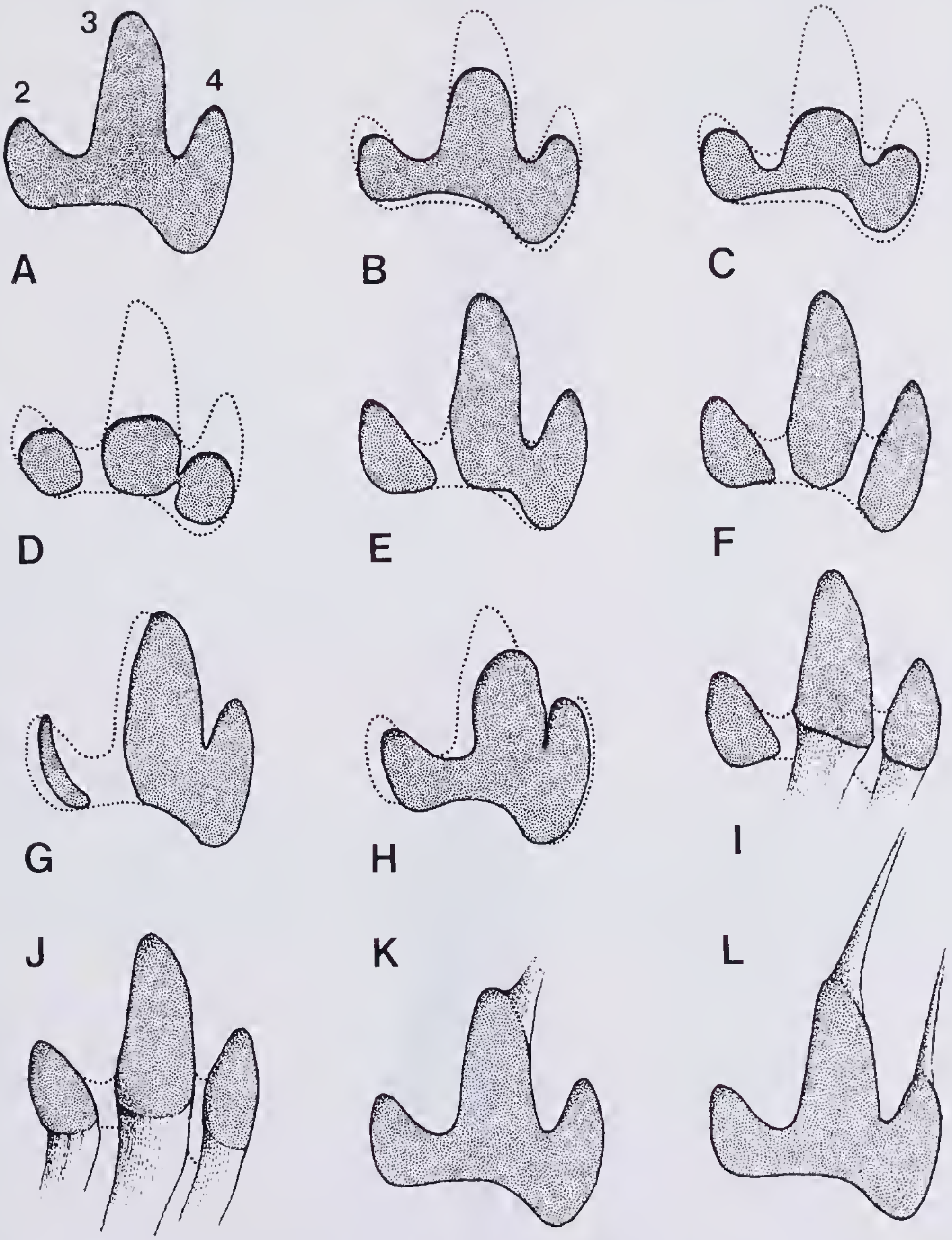


FIGURE 5. Diagrams to illustrate variation in shape of ornithopod footprints (*Wintonopus*) at Lark Quarry. A, complete and undistorted imprint of a right foot; all other diagrams illustrate variation on this basic footprint shape. Examples B, C and D are fore-shortened or 'stubby-toed' footprints formed by the toes entering and leaving the sediment at a steep angle. In example D the toes entered the sediment vertically but did not sink to the level of the interdigital web between digits 2 and 3. In examples E and F the foot has not sunk deeply enough to leave traces of one or both of the interdigital webs. In examples G and H footprint width is reduced because the foot entered and left the sediment obliquely — with the track-maker's weight carried mainly on the outer two digits. Examples I and J show backwardly directed scrape-marks; examples K and L show scrape-marks directed anterolaterally.

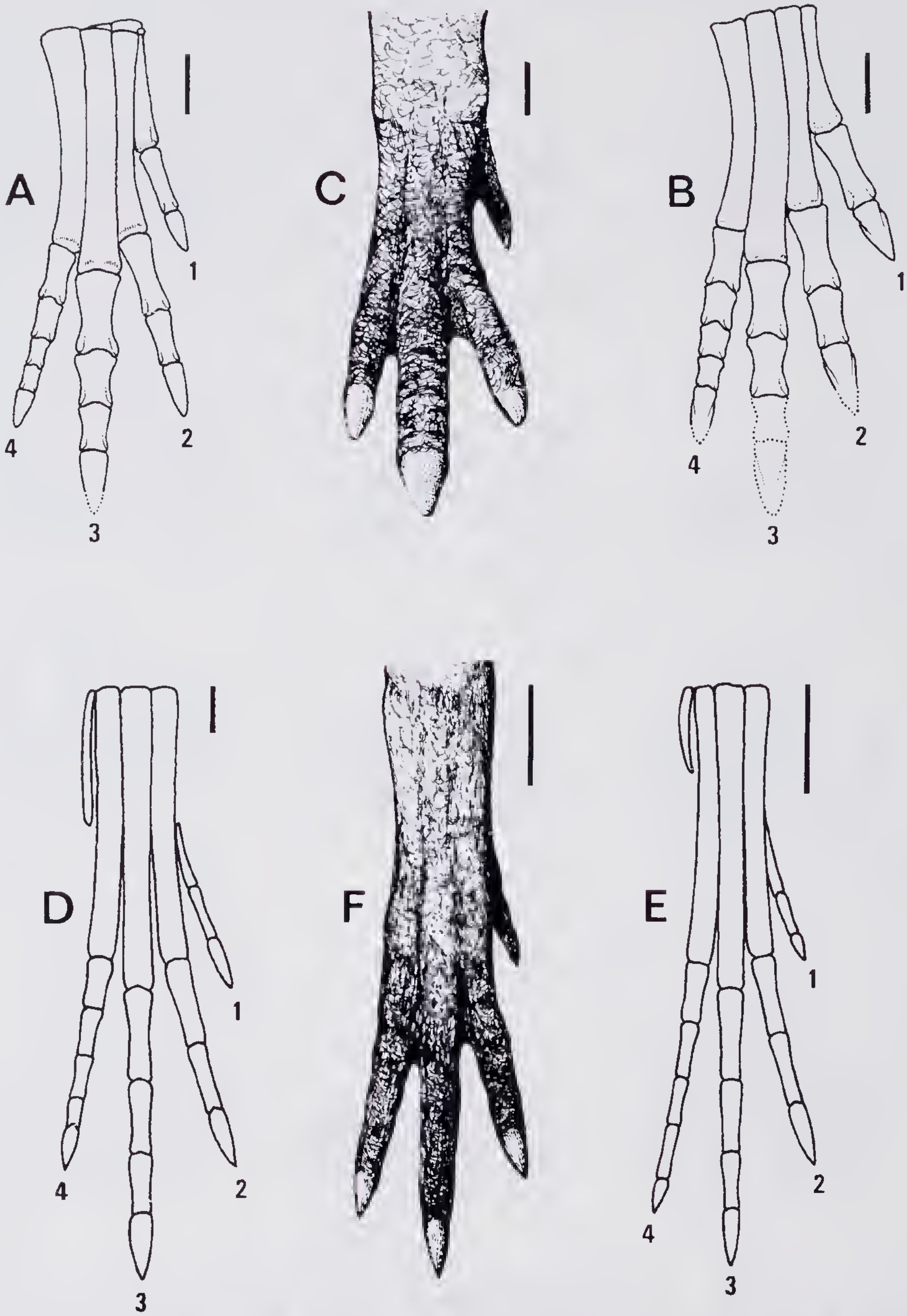


FIGURE 6. Foot structure in small bipedal dinosaurs. In all cases the right foot is shown in anterior view and the scale bar indicates 2 cm. A, foot skeleton in the Upper Jurassic ornithopod *Nanosaurus;* B, foot skeleton in the Lower Cretaceous ornithopod *Hypsilophodon;* C, attempted restoration of foot structure in the *Wintonopus* track-maker (based on mean dimensions in 284 footprints); D, foot skeleton in the Triassic coelurosaur *Coelophysis;* E, foot skeleton in the Upper Jurassic coelurosaur *Compsognathus;* F, attempted restoration of foot structure in the *Skartopus* track-maker (based on mean dimensions in 191 footprints). A and B after Galton and Jensen (1973); D and E after Ostrom (1978).

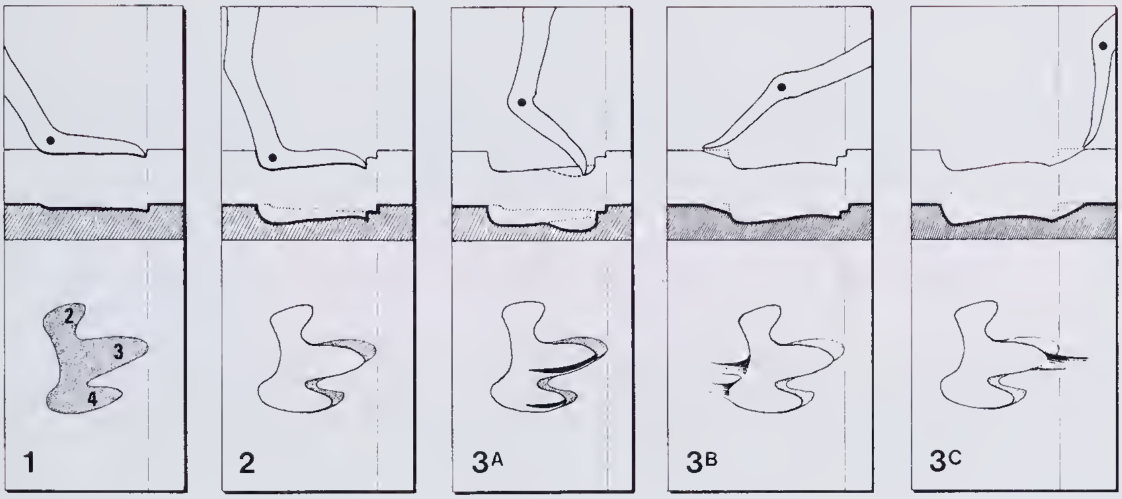


FIGURE 7. Morphological features of ornithopod footprints (*Wintonopus*) related to events during the track-maker's stride cycle. Each diagram shows position of foot (at top, with distal end of metatarsus indicated by a spot), longitudinal section of corresponding footprint (at middle), and corresponding plan view of right footprint (at bottom). Stage 1: start of stride, with forwardly extended foot; initial footprint (shaded) is shallow and shows positive rotation. Stage 2: as the track-maker moves forwards the foot sinks deeper, rotates to face directly ahead, and slips backwards a little (unshaded footprint). Stage 3A: as foot starts to lift from the substrate the toes continue to slip backwards, incising slots in the floor of the footprint. Stage 3B (following Stage 2, or via Stage 3A): toes slip back far enough to breach rear wall of footprint, producing backwardly-directed scrape-marks. Stage 3C (following Stage 2): toes do not slip backwards but drag through front wall of footprint to produce forwardly-directed scrape-marks.

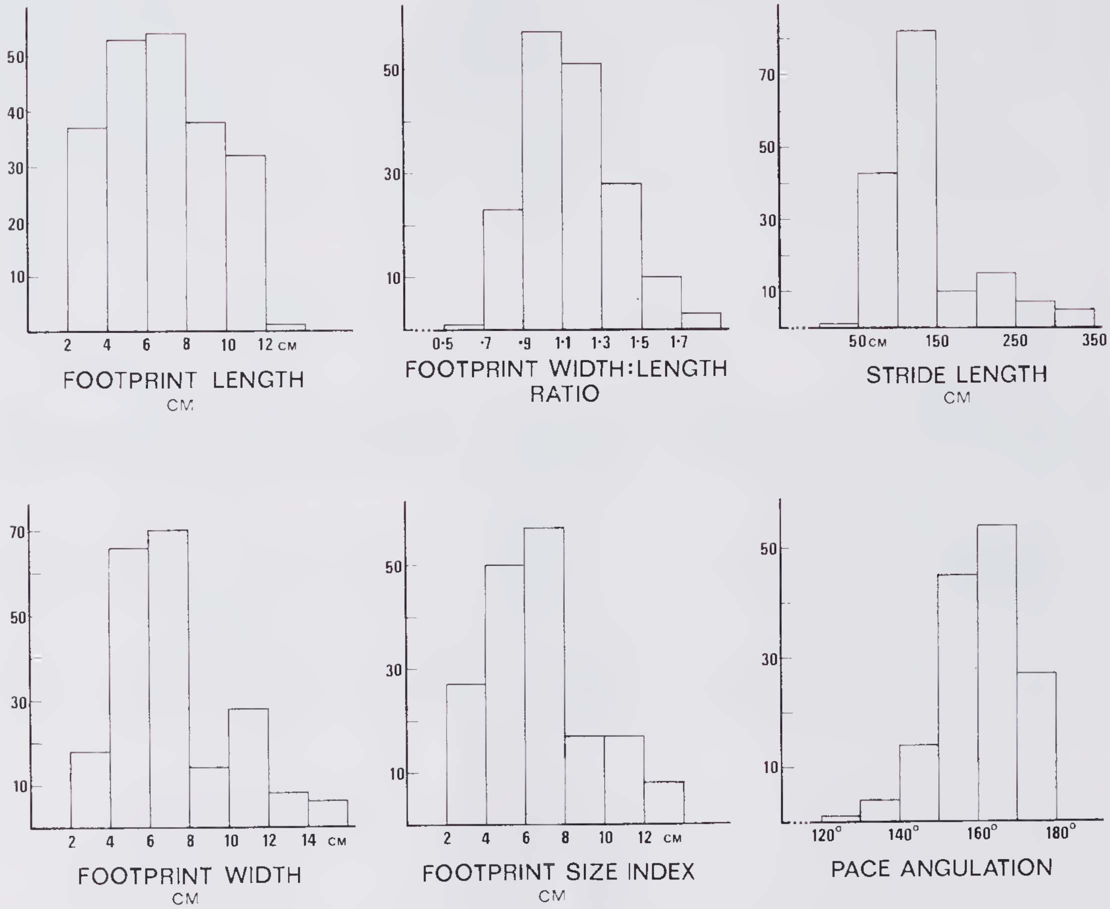
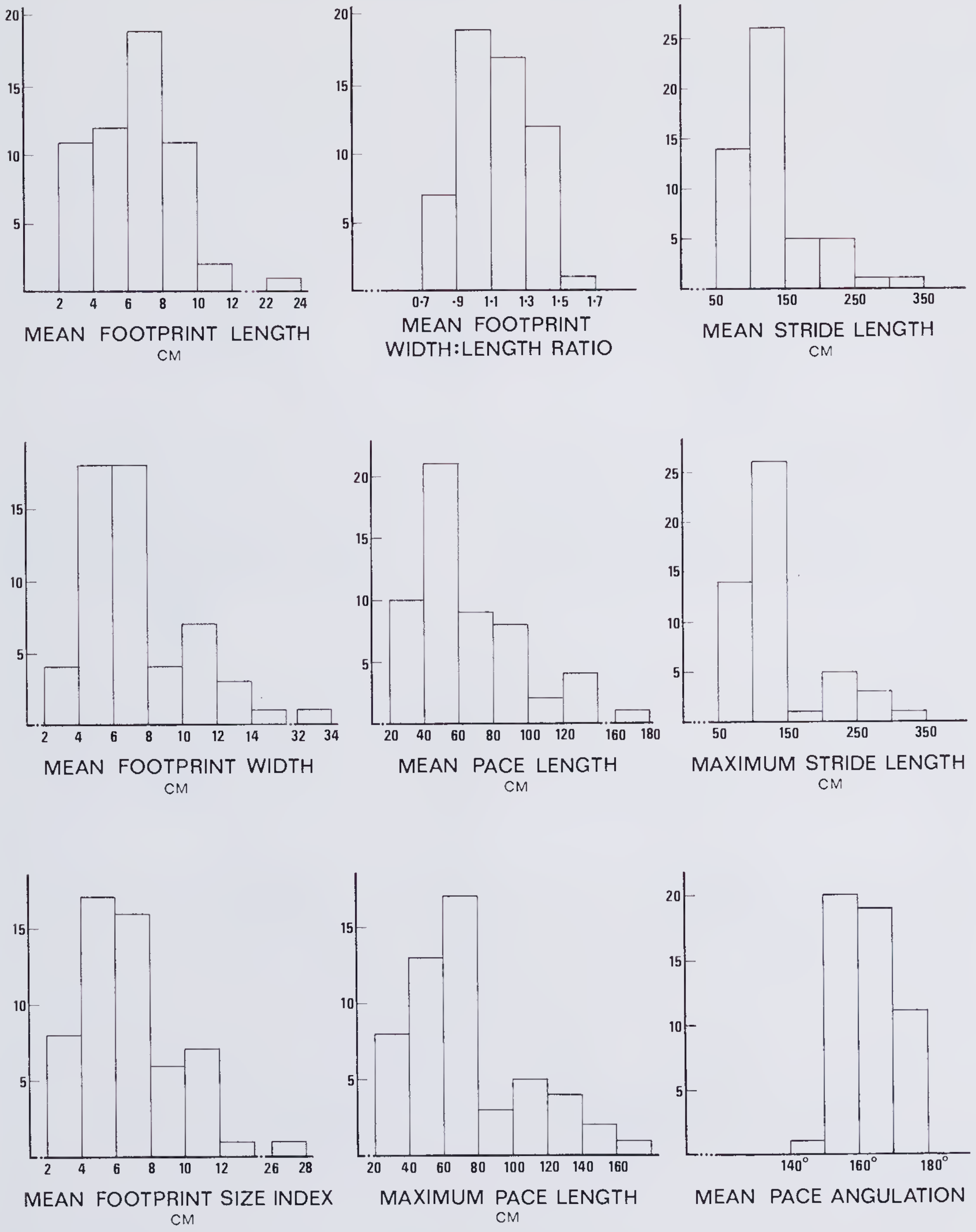


FIGURE 8. Frequency distributions based on pooled data from *Wintonopus* (ornithopod) trackways at Lark Quarry. All modal classes drawn to uniform height, and vertical scales are absolute frequencies. Diagrams for footprint length, footprint width and footprint size index exclude data from single exceptionally large trackway (No. 57 in Table 4; see also Fig. 9).



MEAN FOOTPRINT LENGTH
CM

MEAN FOOTPRINT WIDTH:LENGTH RATIO

MEAN STRIDE LENGTH
CM

MEAN FOOTPRINT WIDTH
CM

MEAN PACE LENGTH
CM

MAXIMUM STRIDE LENGTH
CM

MEAN FOOTPRINT SIZE INDEX
CM

MAXIMUM PACE LENGTH
CM

MEAN PACE ANGULATION

FIGURE 9. Frequency distributions based on grouped data from *Wintonopus* (ornithopod) trackways at Lark Quarry. All modal classes drawn to uniform height, and vertical scales are absolute frequencies.

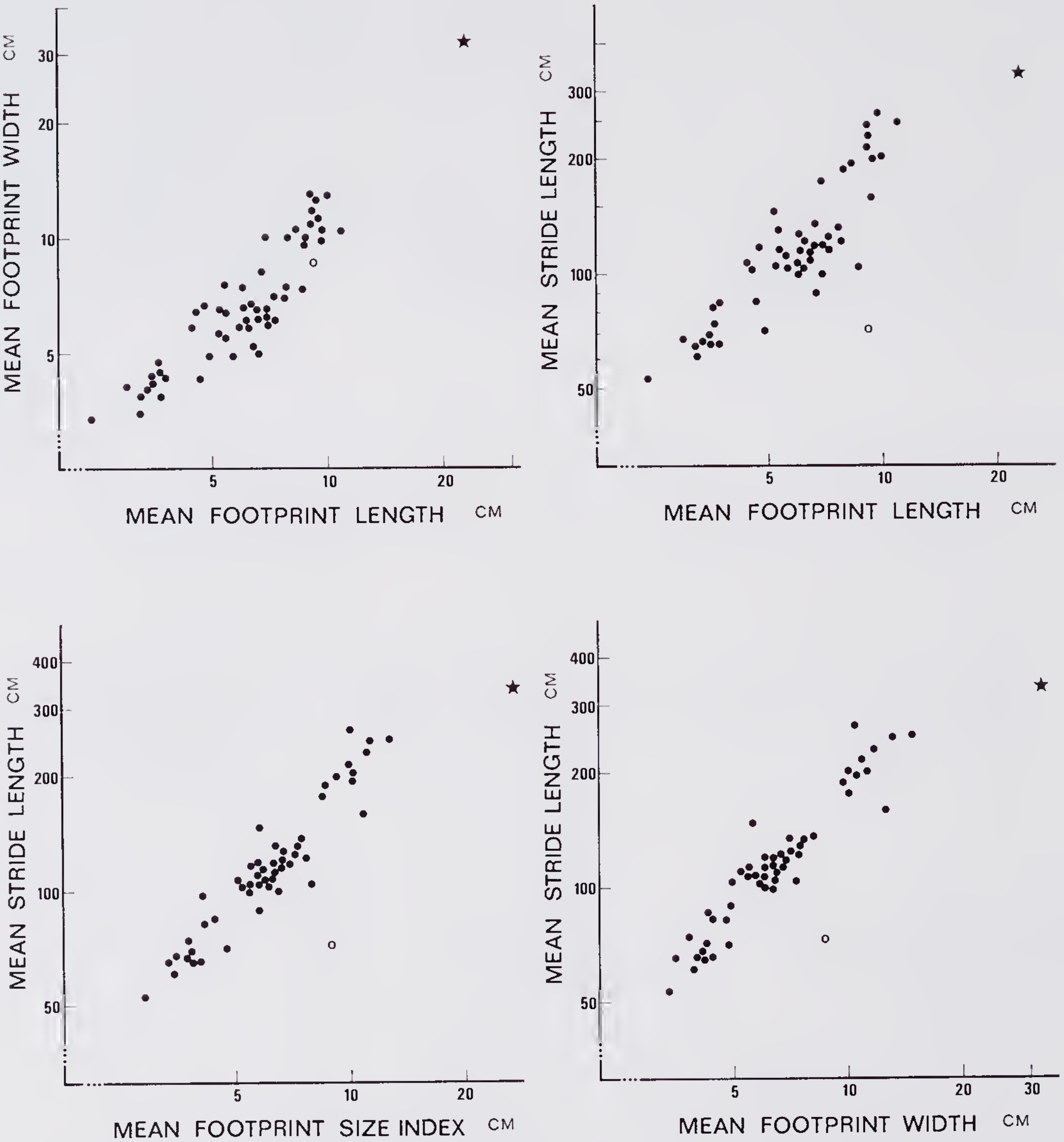


FIGURE 10. Scatter diagrams based on grouped data from *Wintonopus* (ornithopod) trackways. In all cases both axes have logarithmic scales. Note that the New Quarry track-maker (open circle) resembles Lark Quarry track-makers (solid circles) in footprint proportions, but is distinguished by its relatively short stride. The same is true (but less obviously so) for the single exceptionally large track-maker at Lark Quarry (star).

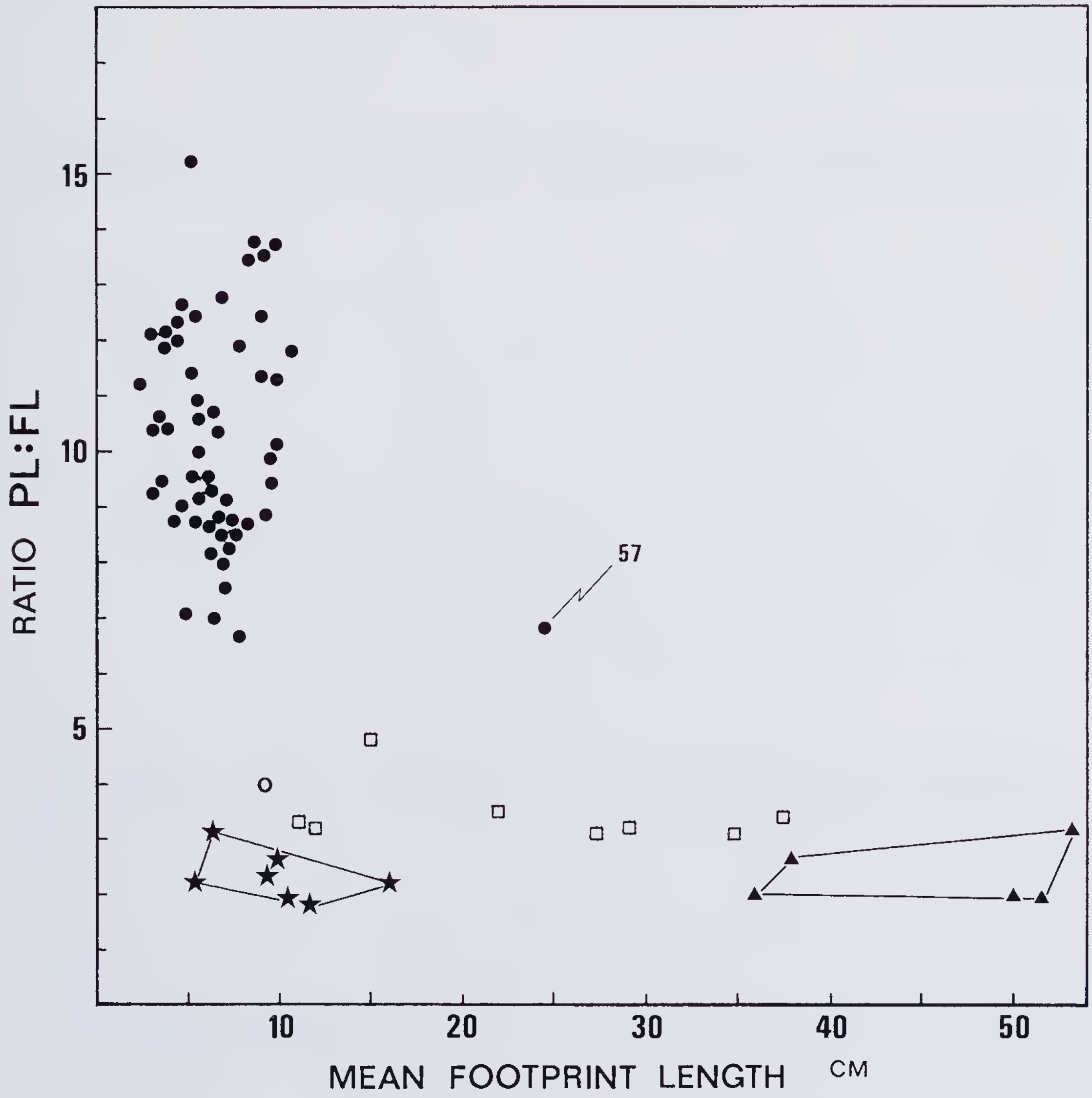


FIGURE 11. Scatter diagram to illustrate relationship between pace length and footprint length in trackways attributed to ornithopod dinosaurs. Solid circles — *Wintonopus* (at Lark Quarry; No. 57 is the single large trackway formed at slightly earlier date); open circle — *Wintonopus* (at New Quarry); stars — *Anomoepus;* triangles — *Irenesauripus;* open squares — various trackways including *Amblydactylus, Gypsichnites* and *Sauropus.* Incorporating data from Sternberg 1932, Lull 1953, Currie and Sarjeant 1979.

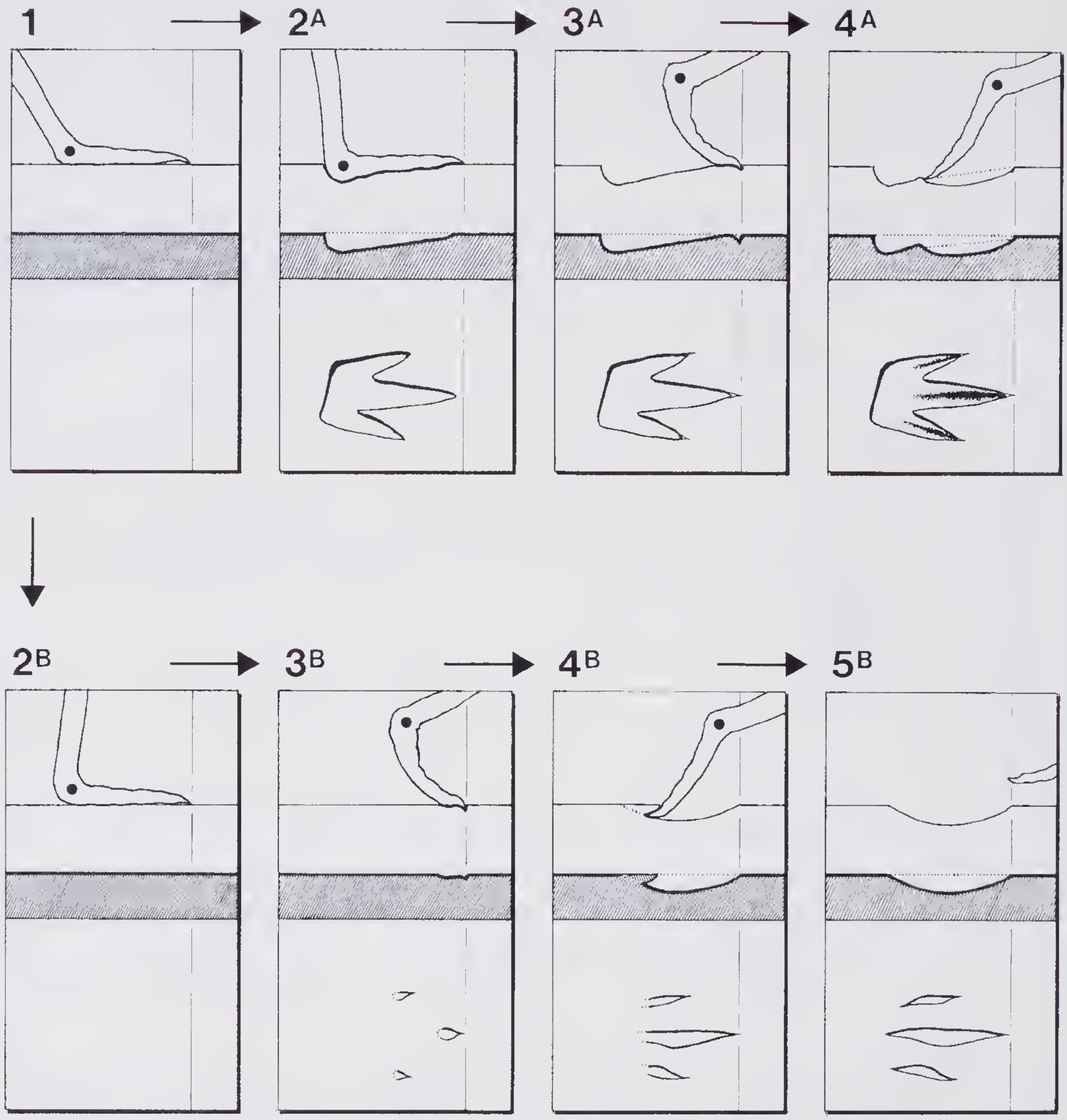


FIGURE 12. Morphological features of coelurosaur footprints (*Skartopus*) related to events during the track-maker's stride cycle. Each diagram shows position of foot (at top, with distal end of metatarsus indicated by a spot), longitudinal section of corresponding footprint (at middle), and corresponding plan view of footprint. Stage 1: start of stride, with forwardly extended foot; initially there is no footprint, or a very shallow one. Stage 2A: as the track-maker moves forwards the foot sinks deeper. Stage 3A: the foot lifts from the substrate, leaving sharp imprints of the claws. Stage 4A (frequently follows Stage 3A): the toes slip backwards, incising slots in the floor of the footprint. The sequence of Stages 2B to 5B is equivalent to the sequence 2A to 4A, but the foot does *not* sink into the substrate; the only traces are scratches produced by the toes slipping backwards.

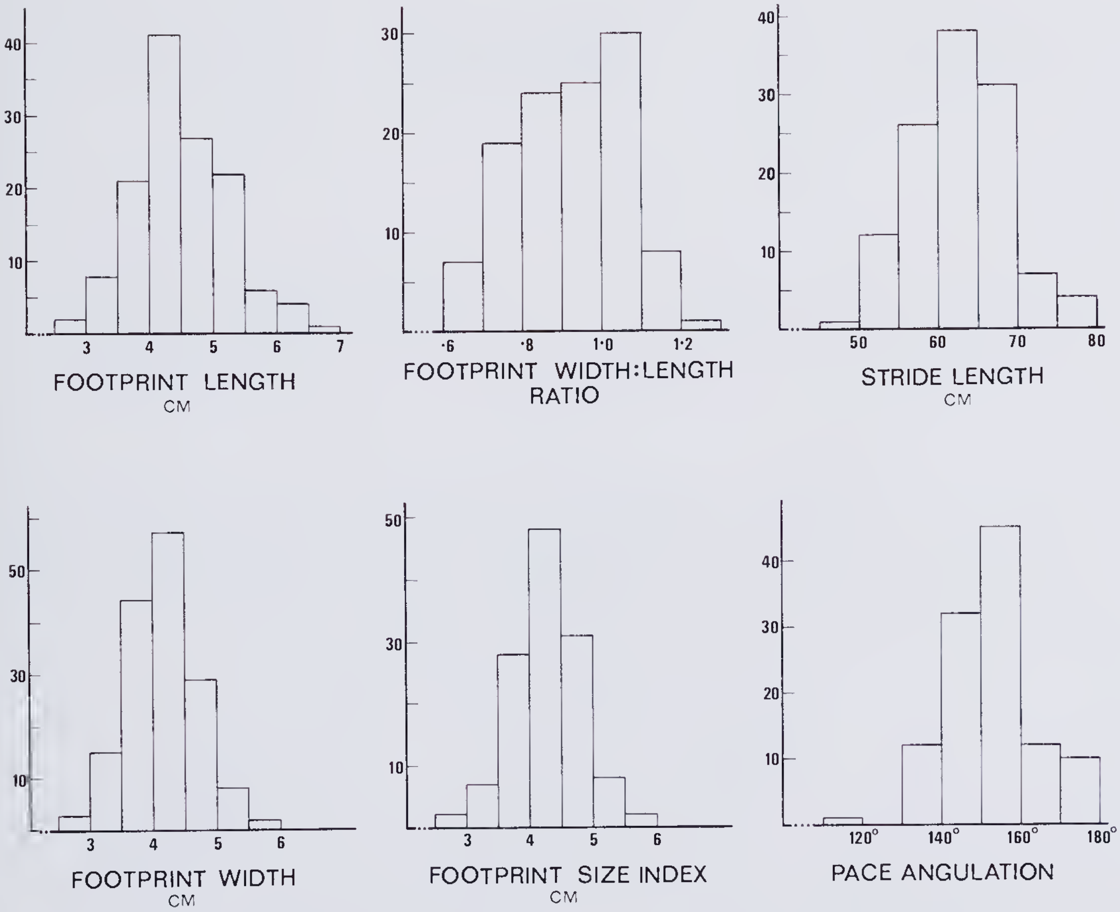


FIGURE 13. Frequency distributions based on pooled data from *Skartopus* (coelurosaur) trackways at Lark Quarry. All modal classes drawn to uniform height, and vertical scales are absolute frequencies.

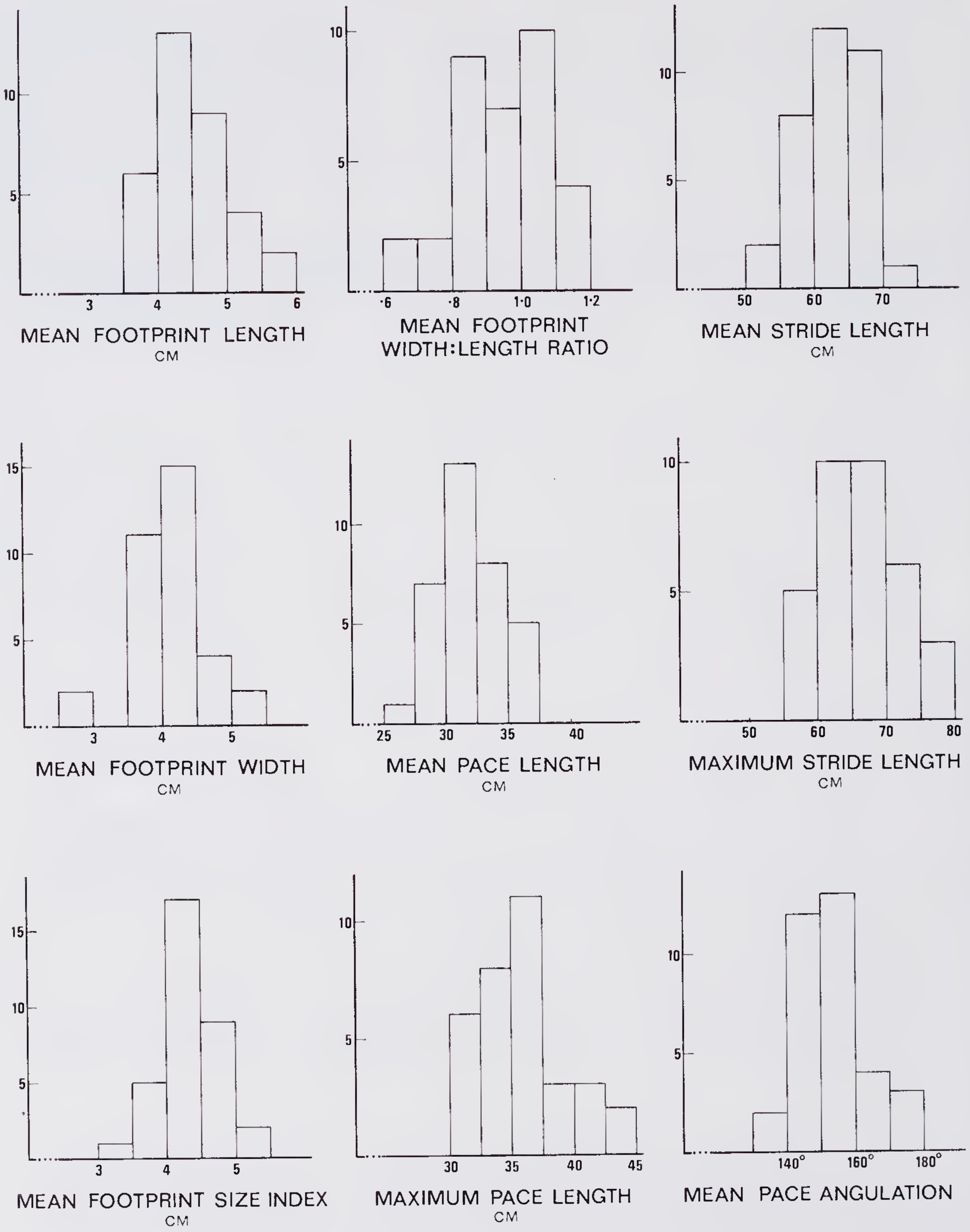


FIGURE 14. Frequency distributions based on grouped data from *Skartopus* (coelurosaur) trackways at Lark Quarry. All modal classes drawn to uniform height, and vertical scales are absolute frequencies.

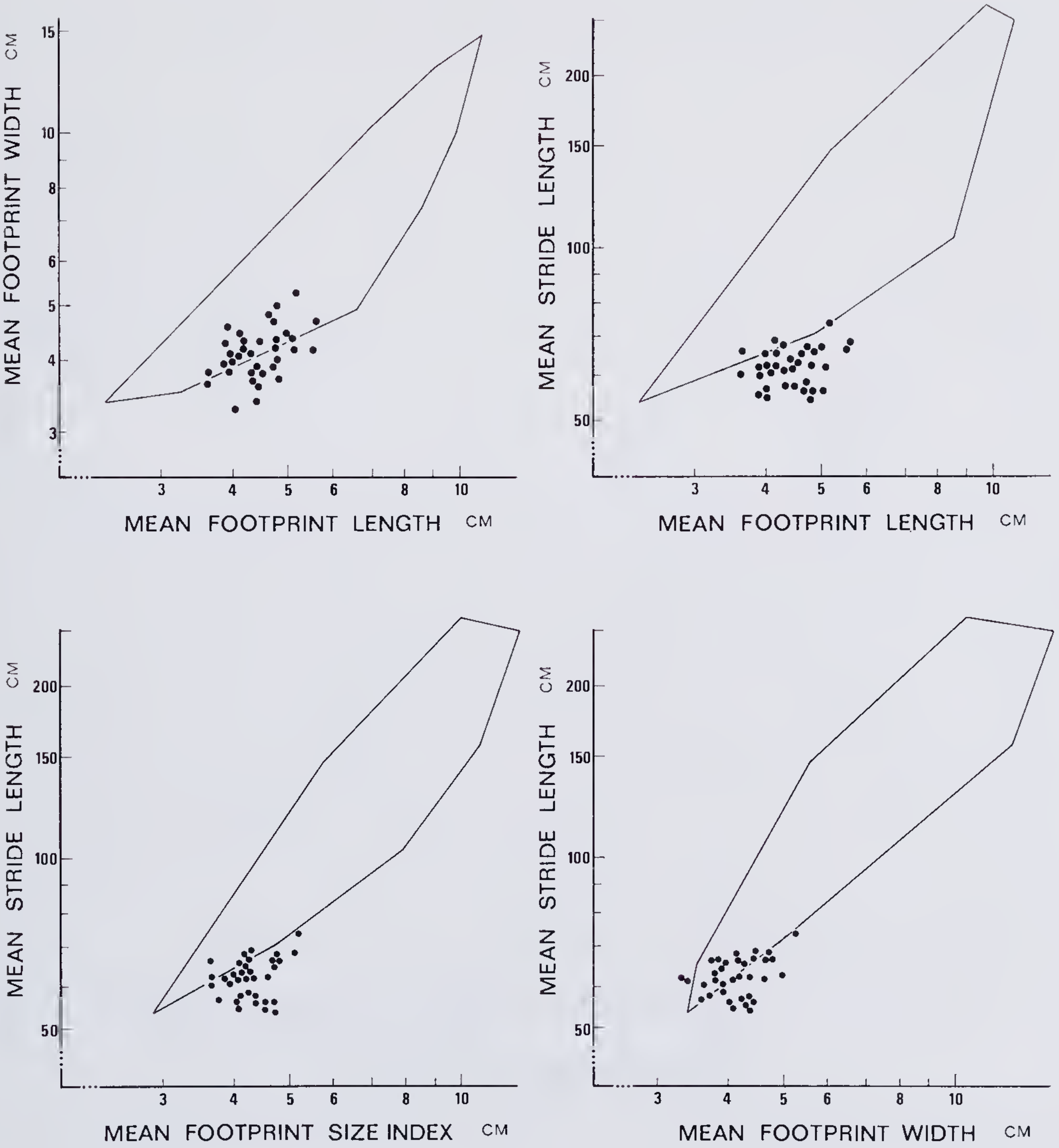


FIGURE 15. Scatter diagrams based on grouped data from *Skartopus* (coelurosaur) trackways at Lark Quarry. In all cases both axes have logarithmic scales. Polygons define distributions for *Wintonopus* (ornithopod) trackways at the same site.

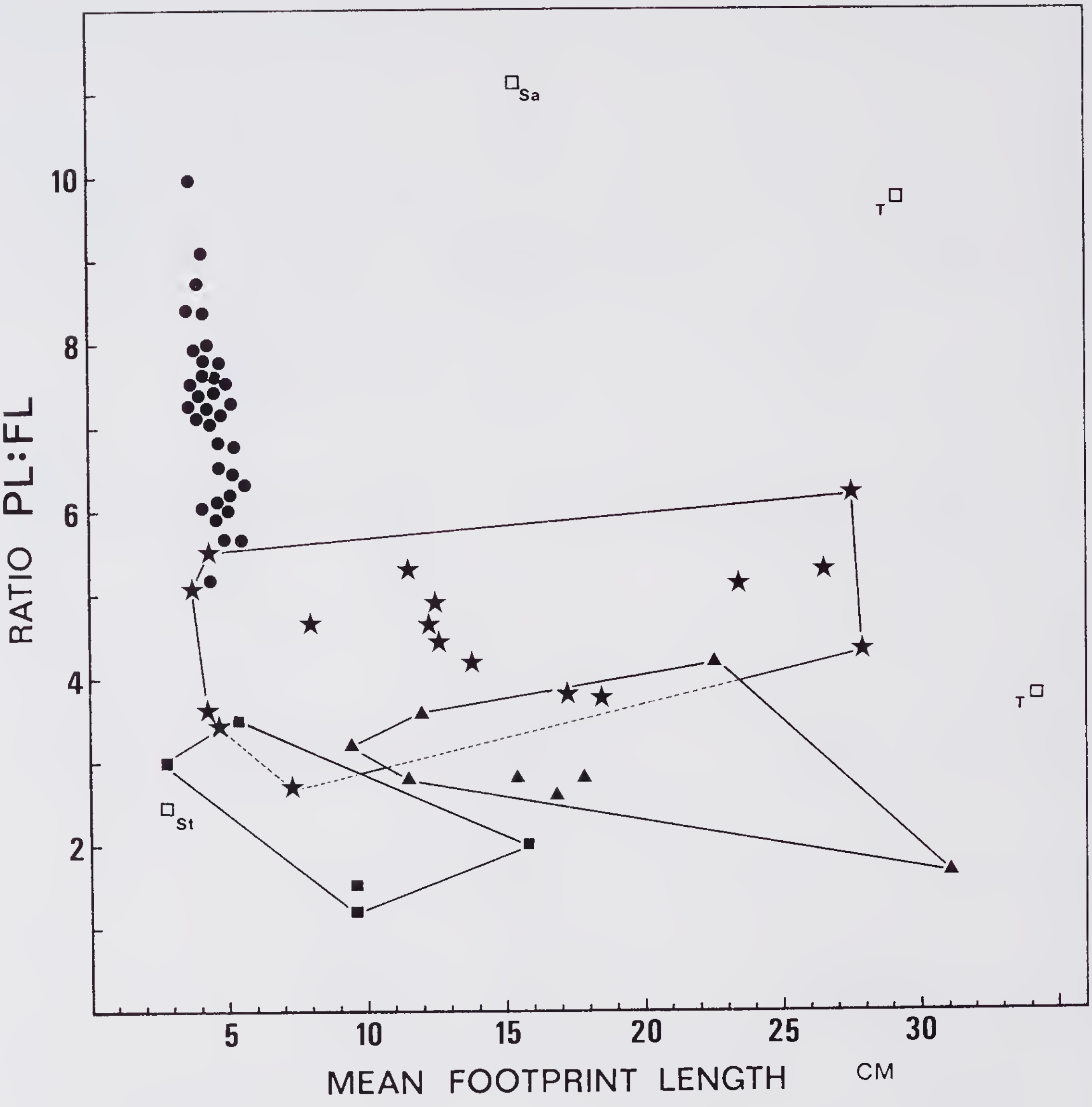


FIGURE 16. Scatter diagram to illustrate relationship between pace length and footprint length in trackways attributed to small and medium-sized theropod dinosaurs. Solid circles — *Skartopus* (at Lark Quarry); stars — *Grallator;* triangles — *Anchisauripus;* solid squares — *Plesiornis;* Sa — *Saltopoides;* St — *Stenonyx;* T — unidentified theropods. Incorporating data from Lull 1953, de Lapparent and Montenat 1967, Bassoullet 1971, Tucker and Burchette 1977, Farlow 1981 (two smallest of 15 unidentified theropods).

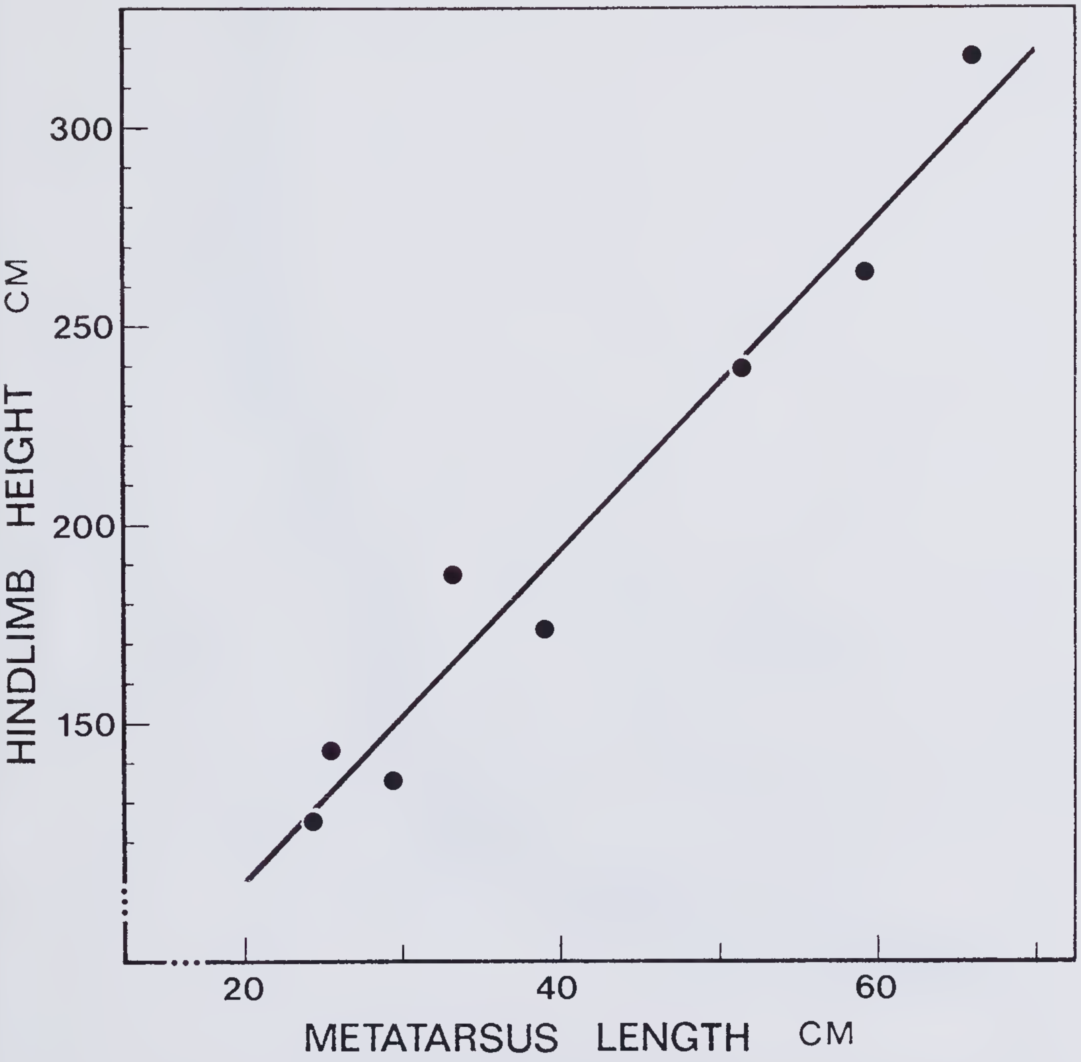


FIGURE 17. Relationship between hindlimb height and metatarsus length in large theropod dinosaurs. Product-moment correlation coefficient (r 0.979) is not improved by transformation of data. Least squares regression line represents equation (*7*) in text. Based on data from Lambe 1917 (*Gorgosaurus*), Osborn 1917 (*Tyrannosaurus*), Gilmore 1920 (*Allosaurus, Ceratosaurus*), von Huene 1932 (*Megalosaurus*), Welles 1954 (*Dilophosaurus*), Russell 1970 (*Daspletosaurus*).

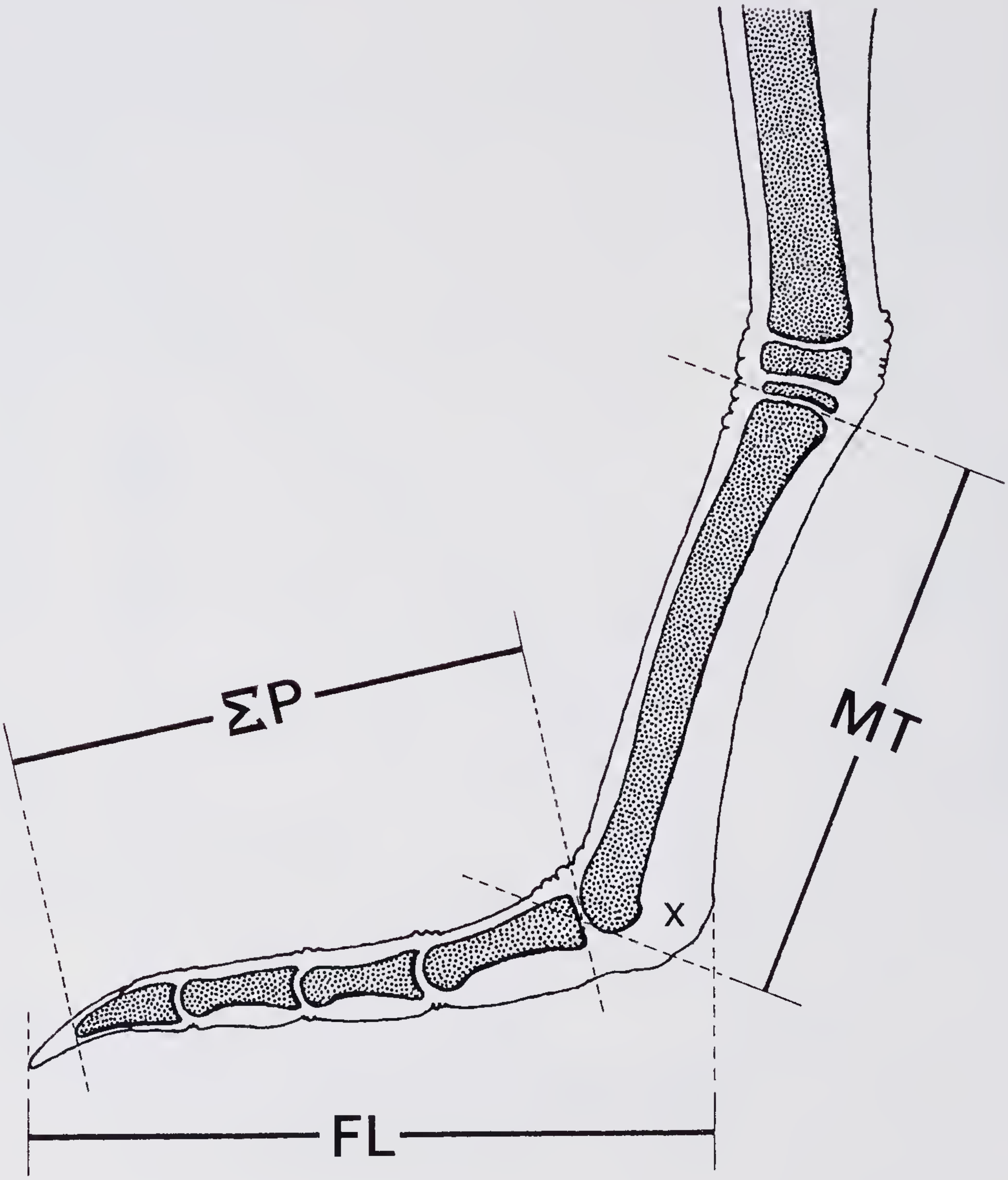


FIGURE 18. Diagrammatic comparison of dimensions in the foot of a bipedal dinosaur. The diagram represents a vertical section along digit 3, with bones stippled and other tissues in outline. ΣP represents the sum of the lengths of phalanges in digit 3. FL (footprint length) comprises ΣP together with claw sheath, joint capsules, base of the metatarsus and (perhaps) a fleshy 'heel' at point X. MT (length of metatarsus) is often about the same length as ΣP.

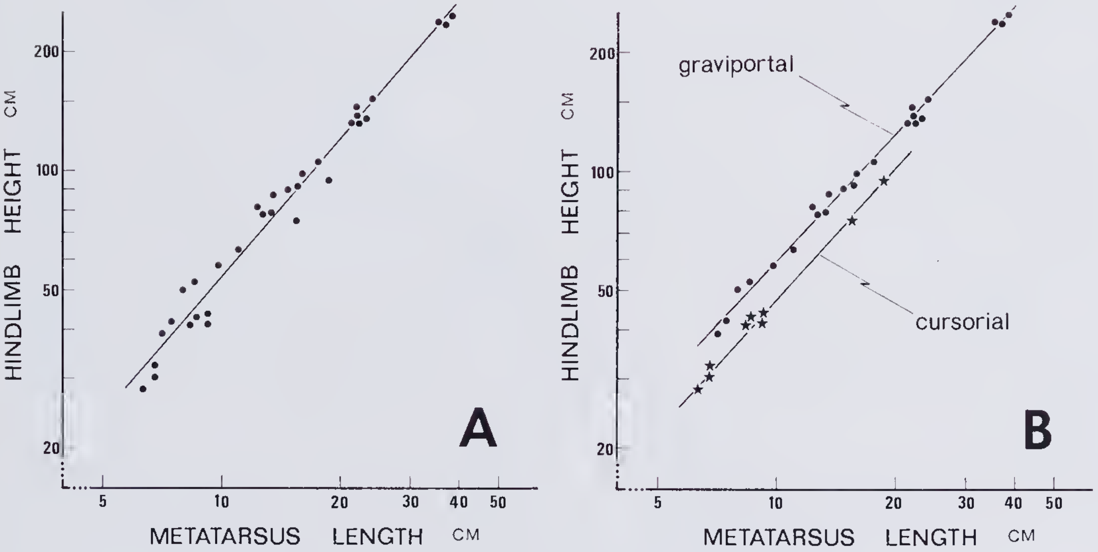


FIGURE 19. Relationship between hindlimb height and metatarsus length in ornithopod dinosaurs. Logarithmic scale on both axes. A, heterogeneous sample of 32 ornithopod dinosaurs; r 0.988; least squares regression line represents equation (*8*) in text. B, same data, but with graviportal ornithopods (23 specimens) separated from cursorial ornithopods (9 specimens); for graviportal ornithopods $r = 0.997$ and least squares regression line represents equation (*10*) in text; for cursorial ornithopods $r = 0.997$ and least squares regression line represents equation (*9*) in text. Based on data from Gilmore 1915 (*Thescelosaurus*) and 1924 (*Stegoceras*), Parks 1920 (*Kritosaurus*), Osborn 1924 (*Protiguanodon, Psittacosaurus*), Hooley 1925 (*Iguanodon*), Lull and Wright 1942 (*Anatosaurus, Corythosaurus*), Thulborn 1972 (*Fabrosaurus*), Galton 1974 (*Hypsilophodon, Dryosaurus, Parksosaurus*), Galton and Jensen 1973 (*Nanosaurus*), Santa Luca et al. 1974 (*Heterodontosaurus*), Dodson 1980 (*Camptosaurus, Tenontosaurus*).

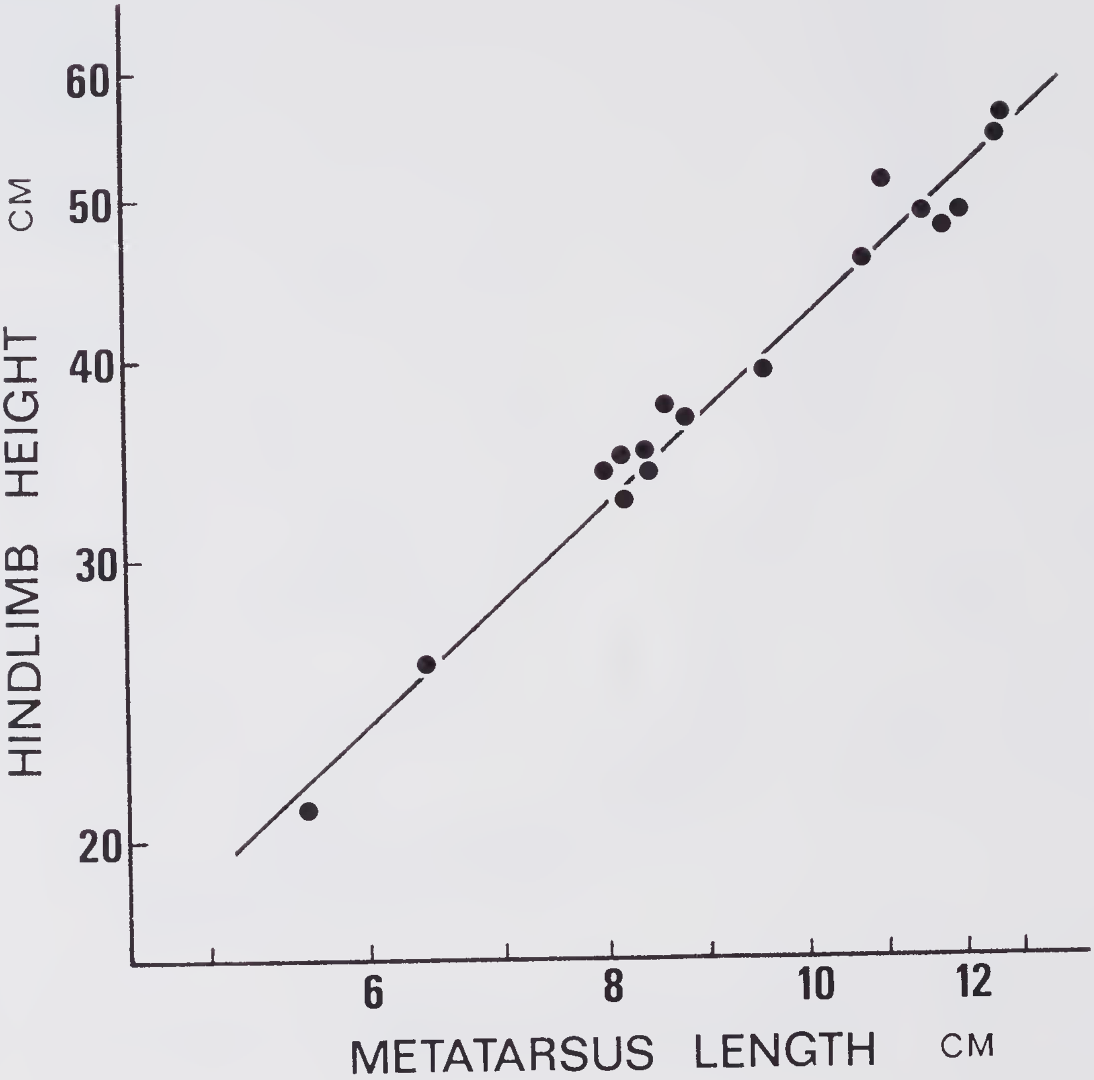


FIGURE 20. Relationship between hindlimb height and metatarsus length in coelurosaurs. Logarithmic scale on both axes; r 0.989, and least squares regression line represents equation (*12*) in text. Based on data from Talbot 1911 (*Podokesaurus*), Osborn 1917 (*Ornitholestes*), Colbert 1964 (*Coelophysis*), Ostrom 1978 (*Compsognathus*).

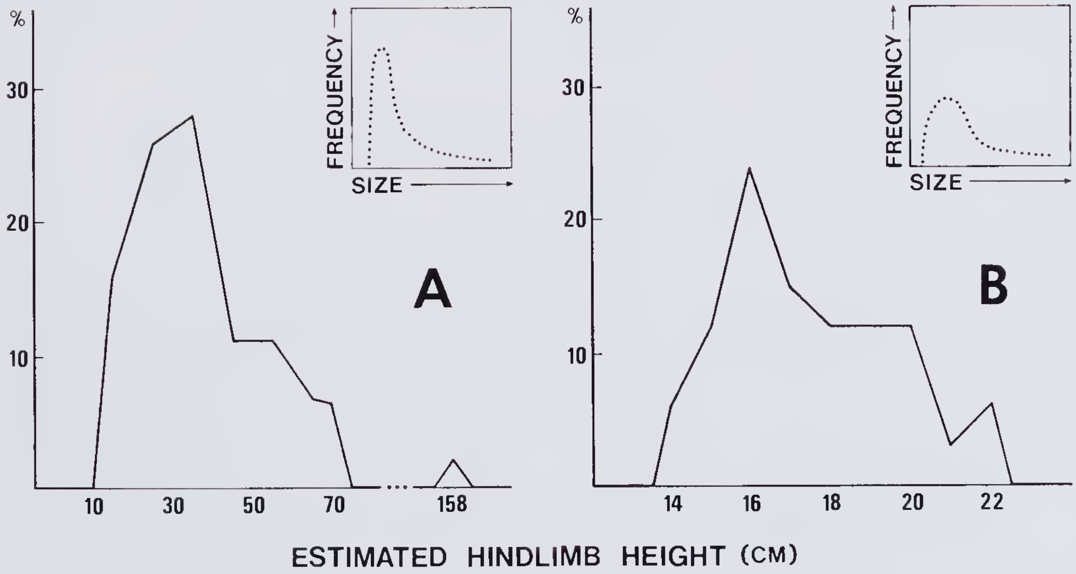


FIGURE 21. Comparison of size-frequency curves for (A) *Wintonopus* track-makers and (B) *Skartopus* track-makers at Lark Quarry. Vertical scale is percentage frequency. Insets show examples of similar curves for populations with different mortality rates and different initial population sizes (adapted from Boucot 1953).

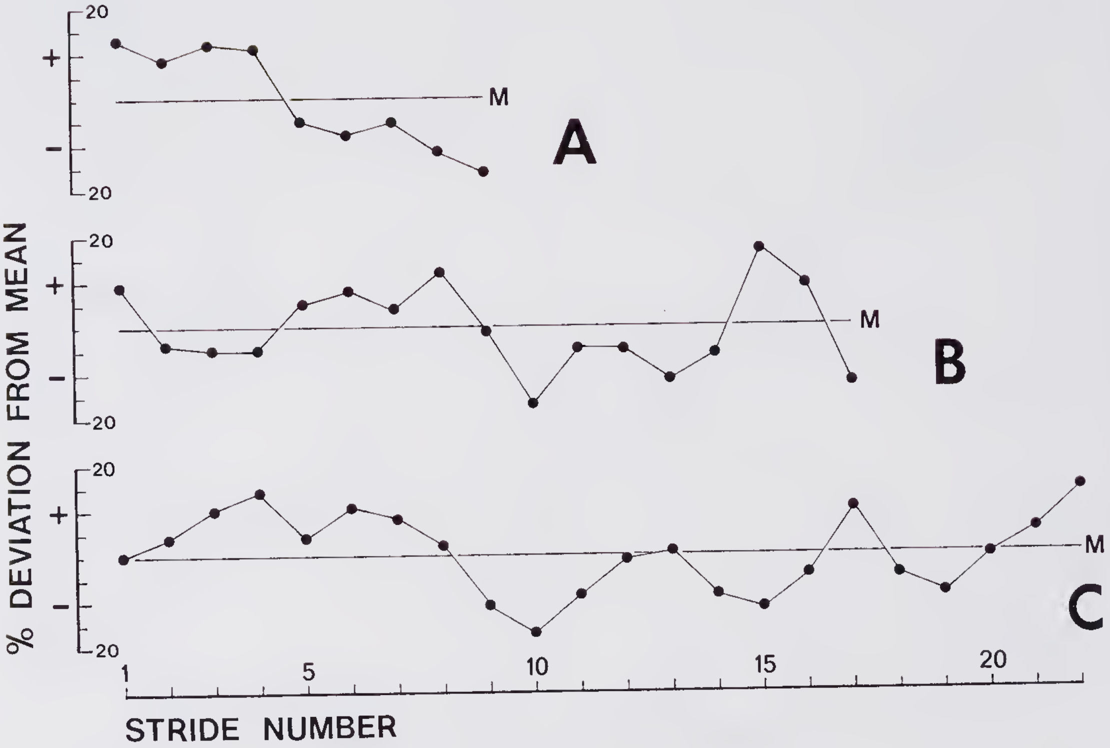


FIGURE 22. Variation in stride length for three track-makers at Lark Quarry. A, carnosaur trackway (cf. *Tyrannosauropus*) comprising 9 strides. B, ornithopod trackway (*Wintonopus*) comprising 17 strides. C, coelurosaur trackway (*Skartopus*) comprising 22 strides. In each case the scale at left indicates percentage deviation from mean stride length (horizontal line, M).

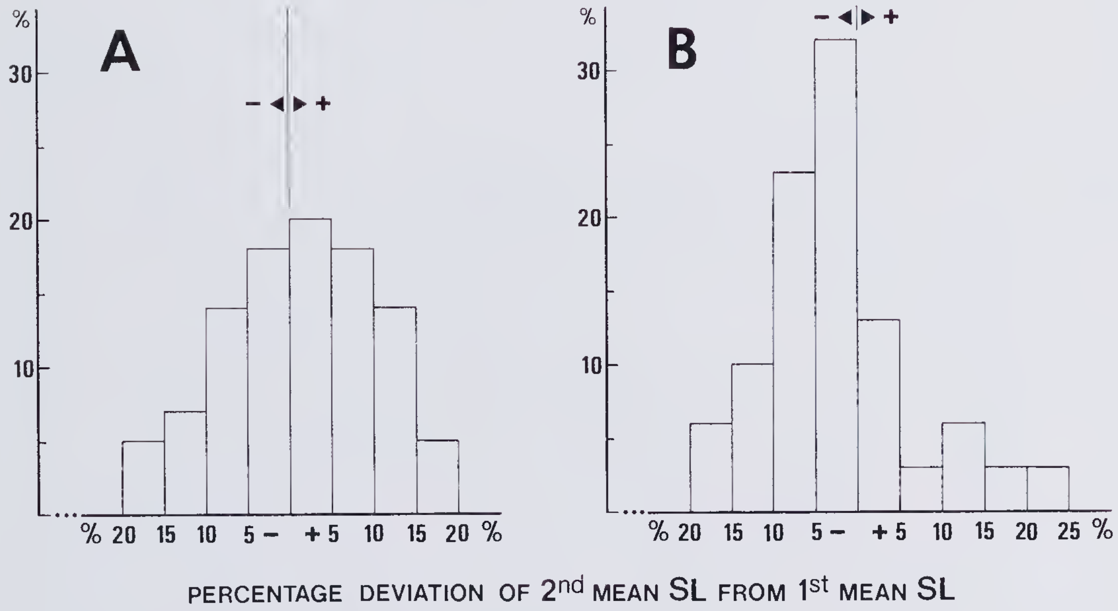


FIGURE 23. Consistency of stride length for (A) 56 *Wintonopus* track-makers and (B) 34 *Skartopus* track-makers at Lark Quarry. Horizontal scale indicates percentage deviation (+/-) of mean stride length for second half of trackway (2nd mean SL) from mean stride length for first half of trackway (1st mean SL). Trackways showing no deviation are shared equally between +(0-5%) and -(0.5%) classes. Vertical scale is percentage frequency.

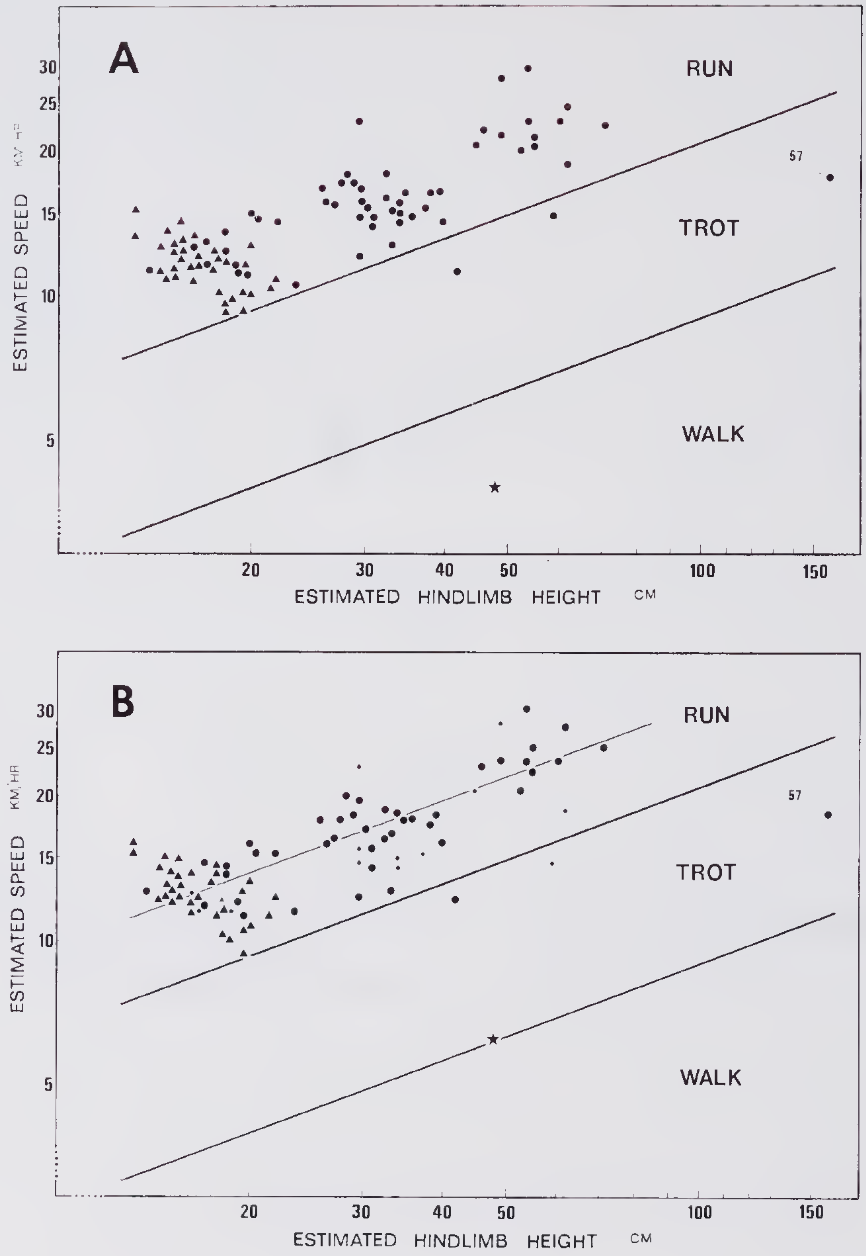


FIGURE 24. A, relationship between estimated mean speed and estimated hindlimb height for *Wintonopus* track-makers (solid circles) and *Skartopus* track-makers (triangles) at Lark Quarry. For the single *Wintonopus* track-maker at New Quarry (star) speed is estimated with equation (*6*) in text. Logarithmic scale on both axes. Lines defining gaits correspond to size/speed relationships when λ/h is 2.0 (walk-trot transition) and 2.9 (trot-run transition). B, relationship between estimated hindlimb height and estimated *maximum* speed (based on single longest stride per trackway). Small symbols indicate that maximum speed is also mean speed (i.e. all strides in trackway are equal in length, or only a single stride could be measured). Speed for the New Quarry track-maker (star) is maximum possible estimate, derived (perhaps inappropriately) with equation (*11*) in text. Line drawn through distribution indicates the *theoretical* regression of speed on hindlimb height when λ/h is 3.93.

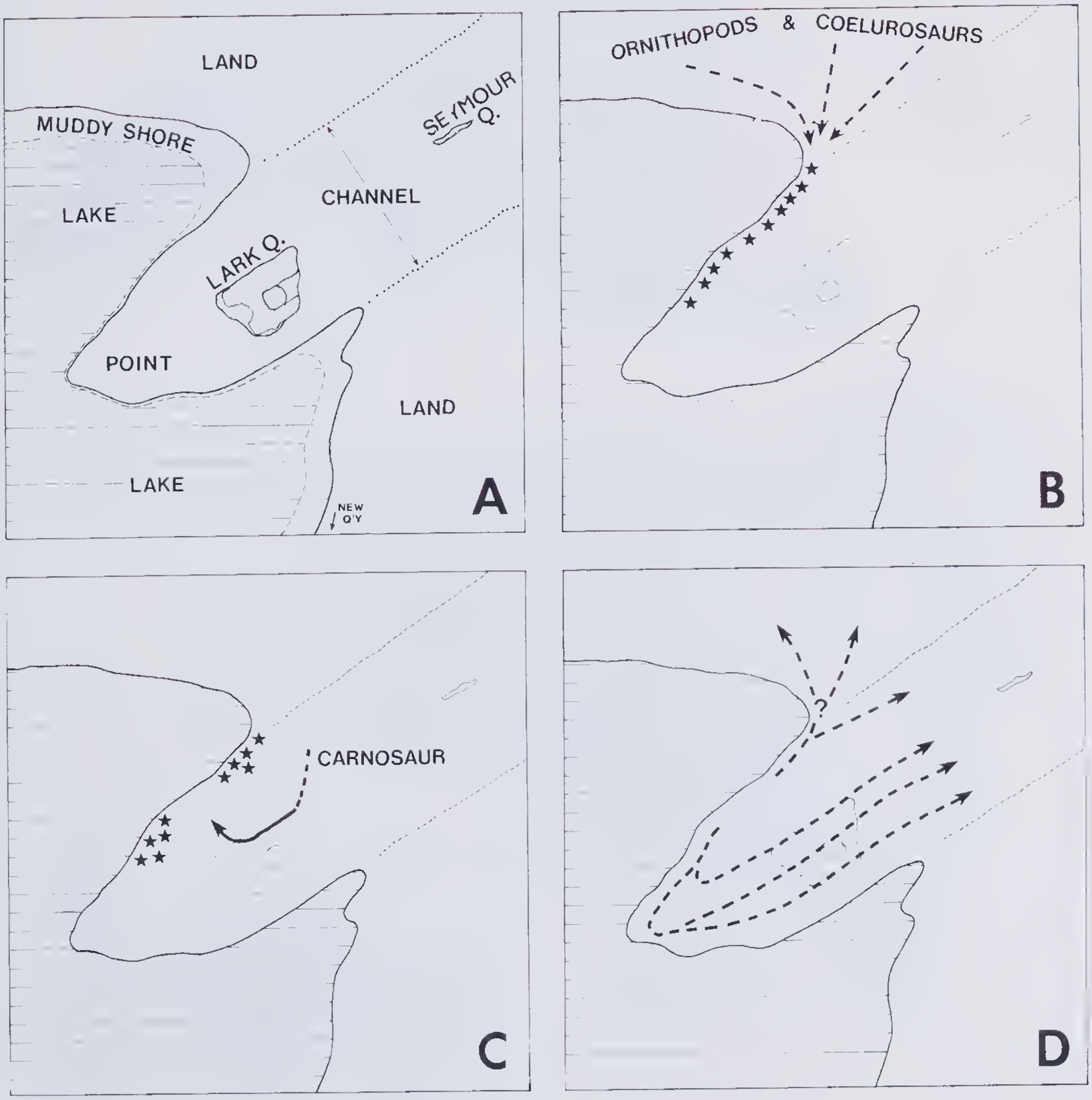


FIGURE 25. Reconstruction of geographic features and events leading to formation of the Lark Quarry trackways. A, outline reconstruction of geographic features at the time the trackways were formed. Sites of Lark Quarry and Seymour Quarry are superimposed. B, ornithopods and coelurosaurs congregate to drink or to forage in the area marked by stars (possibly also further to SW). C, carnosaur traverses future site of Lark Quarry from NE to SW; it turns sharp right to approach the ornithopods and coelurosaurs, which begin to disperse. D, ornithopods and coelurosaurs take fright and stampede, presumably on account of carnosaur's subsequent behaviour (unknown); some may escape via their entry route (?), but at least 150 are driven round the point to the SW and can only escape by running to the NE — across the future sites of Lark Quarry and Seymour Quarry.

PLATE 1

Wintonopus latomorum ichnogen. et ichnosp. nov.,
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, preserved as natural casts at Seymour Quarry. All × 1.0.

FIGURES A–B: *Wintonopus latomorum;* right footprint in posterior (A) and inferior (B) views. The specimen is a natural cast detached from overlying sandstone. Distal parts of all three digits are broken away; so too is the inferior part of digit 3 (which in Fig. B reveals sandstone filling and ironstone cortex). Adherent tubular structures are plant rootlets and/or burrows of invertebrates. Fine tubercles and wrinkles may represent skin texture. In Fig. B note concave posterior margin (uppermost). (QM F12264).

FIGURES C–D: *Skartopus australis;* right footprint in inferior (C) and anterior (D) views. A natural cast still attached to a small portion of overlying sandstone. (QM F12265).

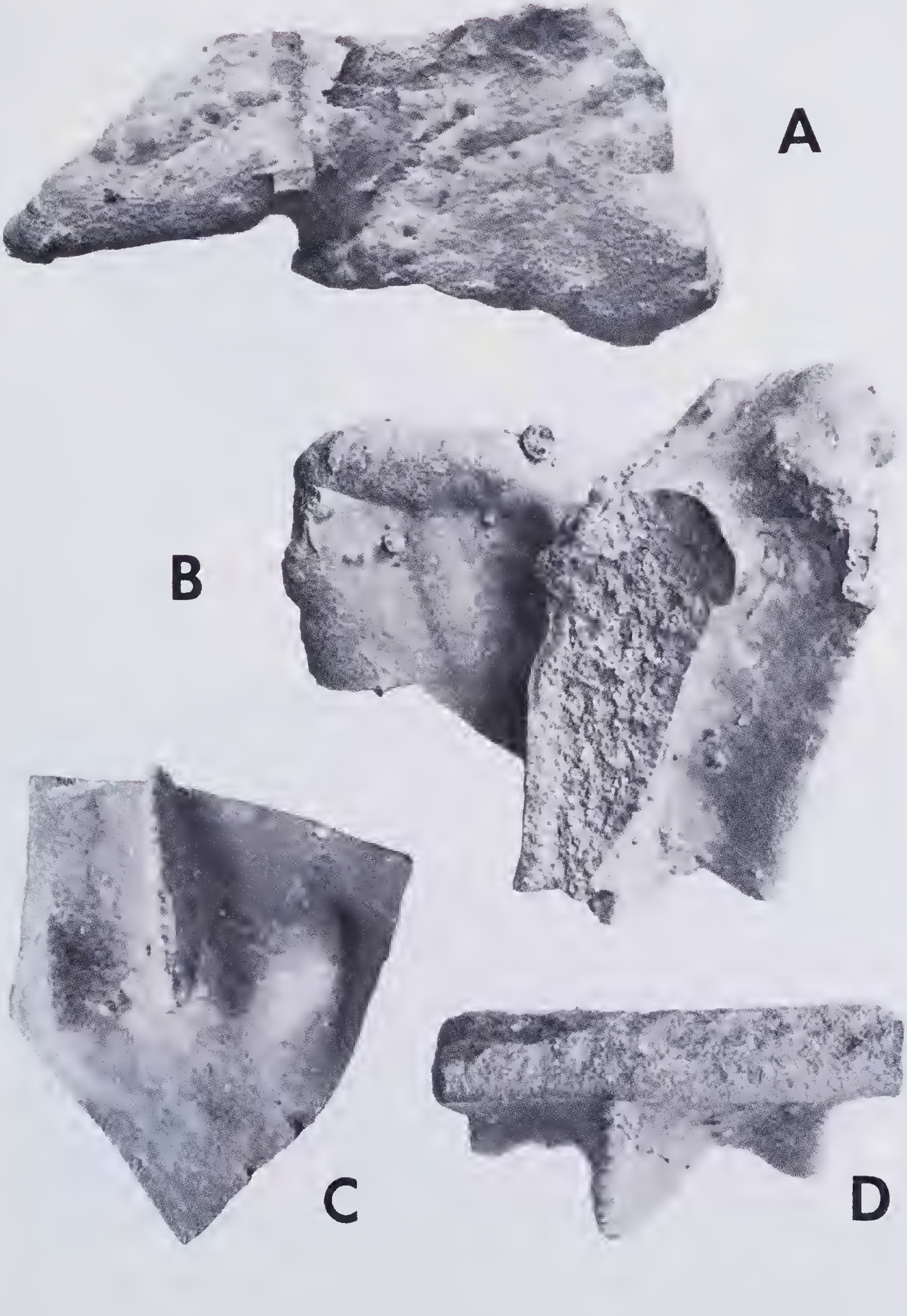

A
B
C
D

PLATE 2

Sediments at Lark Quarry.

FIGURE A: Freshly-broken hand-specimen showing finely laminated claystone in which dinosaur footprints occur as natural moulds. Dark-coloured sediment below the level of the scale-bar (marked in cm) is part of the underlying sandstone.

FIGURE B: Natural section (joint face) through laminated claystone and the underlying sandstone bed. Scale bar marked in cm. Colour contrast between claystone and sandstone is slightly masked by iron-staining (especially at upper left). The three slot-like cavities (across centre) are pick-marks.

Abbreviations: *a*, thin ferruginous adhesion from overlying sandstone; *f*, dinosaur footprint, still filled with overlying sandstone; *t*, tubular structures (possibly escape burrows of arthropods).

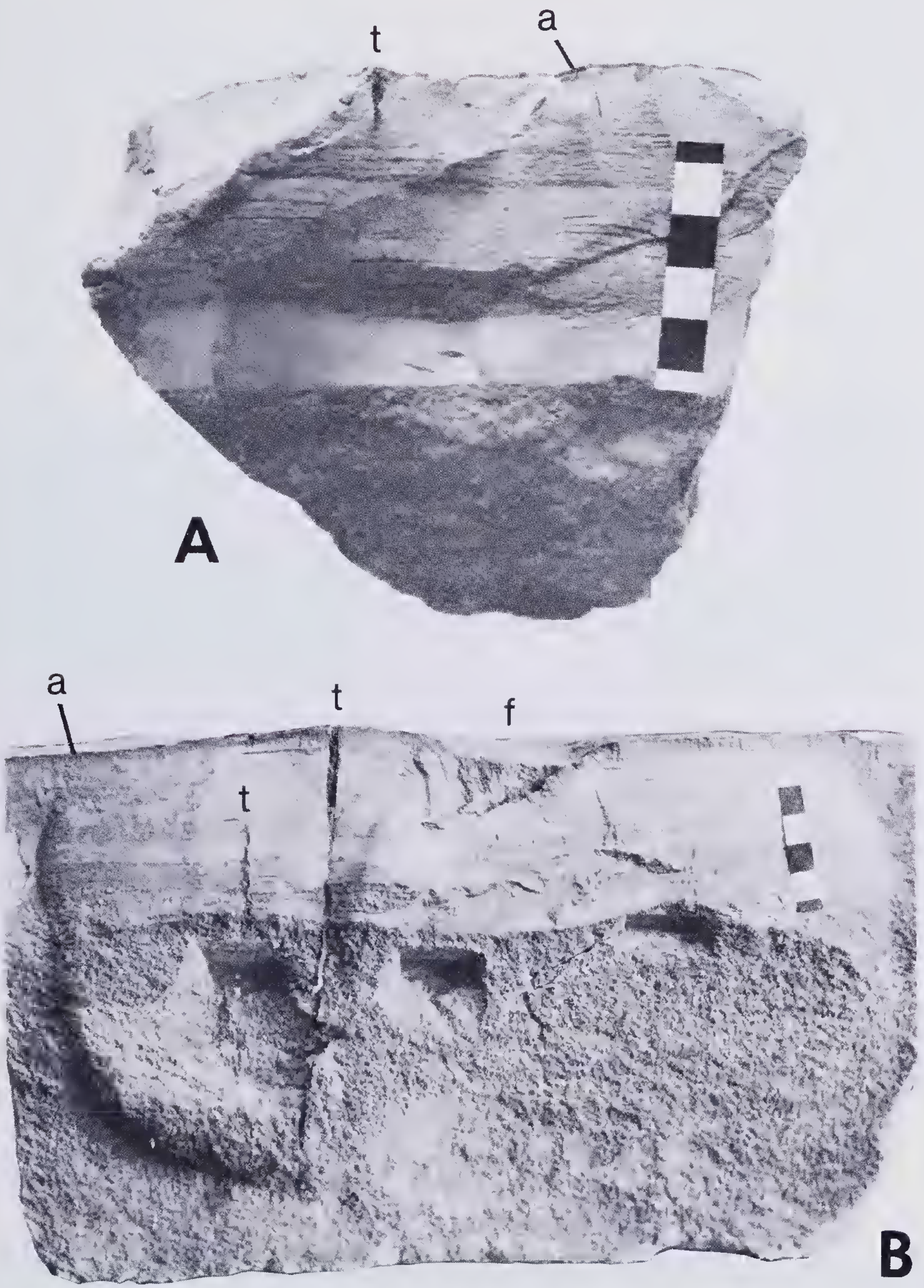

t
a
A
a
t
f
t
B

PLATE 3

Lark Quarry, viewed from the NW. Carnosaur footprints (cf. *Tyrannosauropus*) are visible in front of kneeling figure at centre. The site is now roofed for its protection.

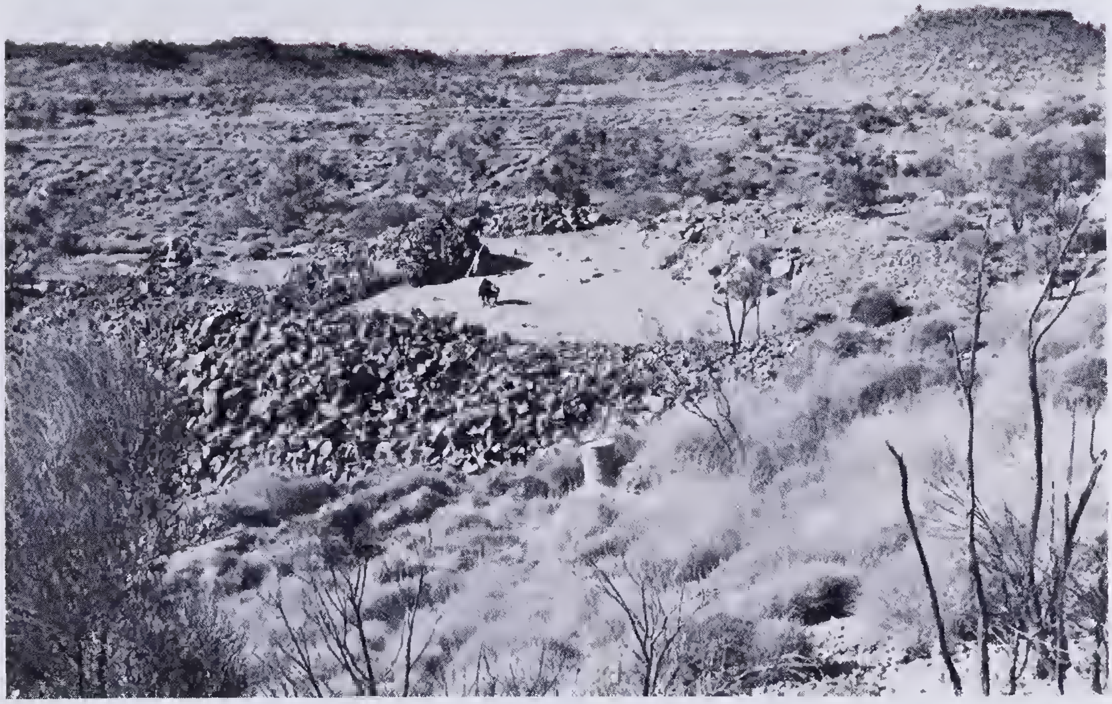


PLATE 4

Portion of Lark Quarry bedding plane to show abundance, relative sizes and orientation of dinosaur footprints. All footprints are natural moulds, and lighting is from the lower left. Area shown is near the W corner of the quarry (see Fig. 3 in text) and is approximately 2.8 by 3.8 m. The sequence of three large footprints (numbered 6 to 8) is from the trackway of a carnosaur that travelled to the SW (towards bottom of page). The numerous small footprints (350+) are attributed to coelurosaurs and small ornithopods, all of which travelled in the opposite direction.


6
7
8

PLATE 5

Carnosaur footprints, cf. *Tyrannosauropus.*

FIGURE A: Single left footprint preserved as natural mould, × 0.22. Photographed from fibreglass replica (QM F10322/I), lighting from N. This is footprint number 3 in the carnosaur trackway (11 prints) at Lark Quarry. Note ripples of sandy sediment in the floor of the print, and surrounding footprints of small dinosaurs.

FIGURE B: Portion of Lark Quarry bedding plane (NW margin) showing first four footprints in carnosaur trackway. Photographed obliquely under natural low-angle illumination. Scale indicated by stride of the carnosaur (3.31 m or approximately 11 feet). The animal moved from NE (top right) to SW (lower left); note the upwelling of sediment around each footprint, and the numerous footprints of small dinosaurs that moved in the opposite direction.

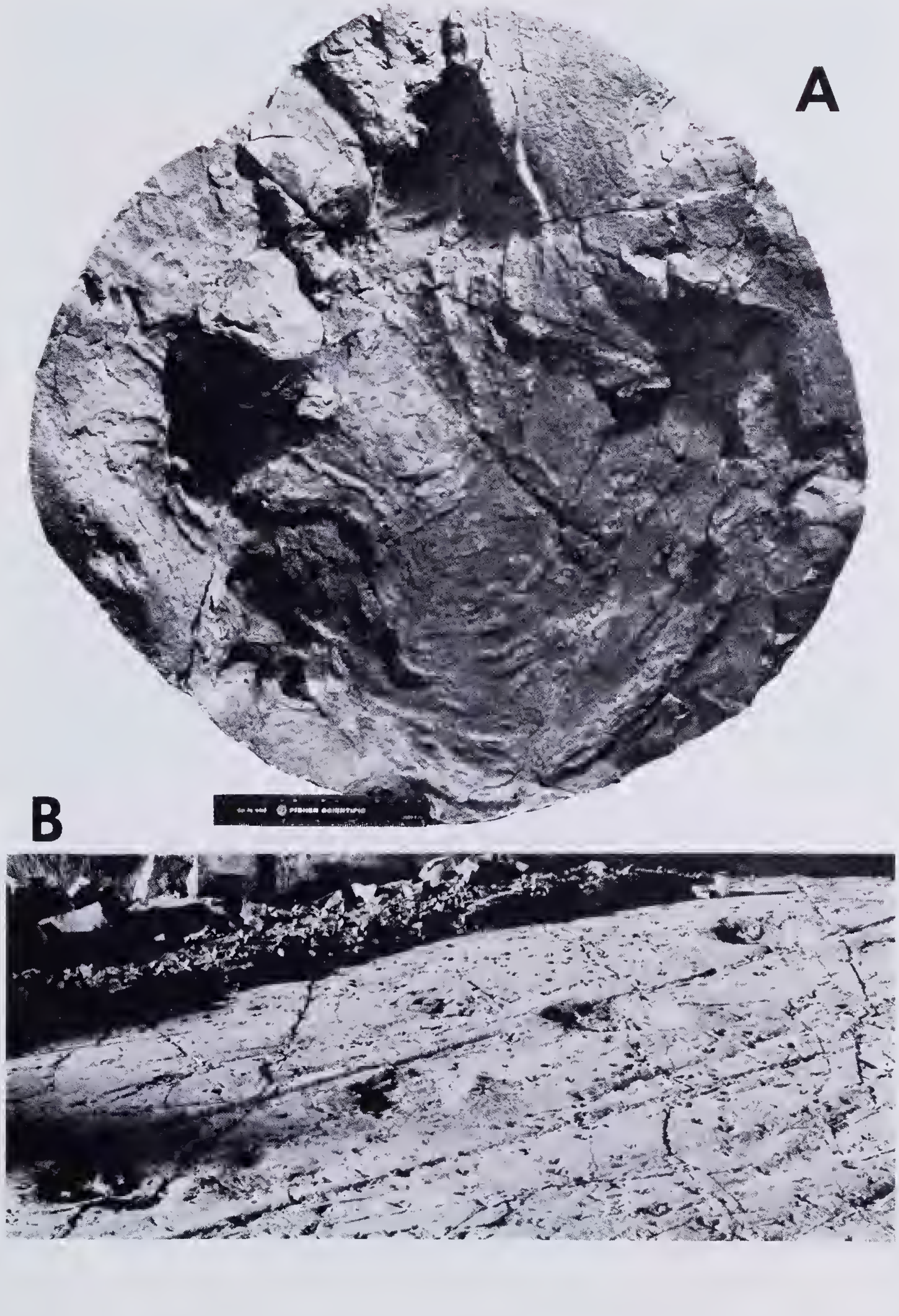

A
B
FISHER SCIENTIFIC

PLATE 6

Carnosaur footprint, cf. *Tyrannosauropus.*

Single left footprint preserved as natural mould, × 0.25. Photographed from fibreglass replica (QM F10322/II), with lighting from NW. This is footprint number 7 in the trackway at Lark Quarry. In diagrammatic key (below): ART, artefact (a pick-mark); ORN 1, ornithopod footprint still filled with sandstone; ORN 2, ornithopod footprint with scrape-marks extending forwards from digits 3 and 4. All other footprints appear to be those of coelurosaurs.

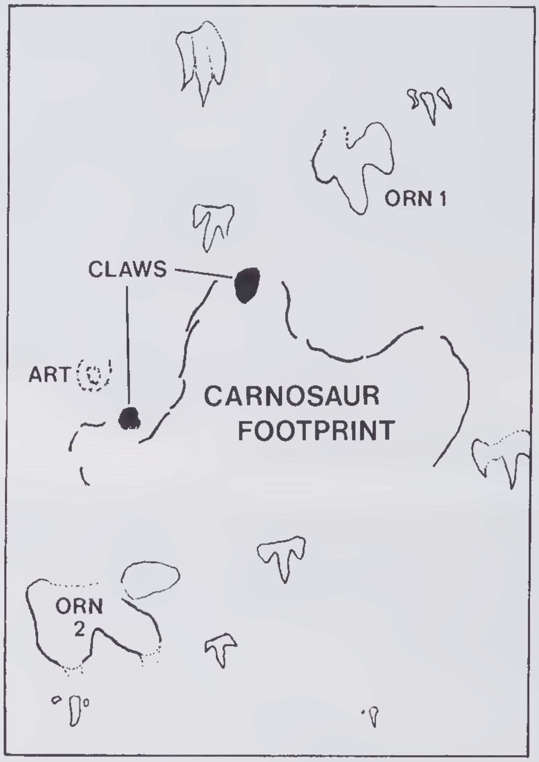


PLATE 7

Wintonopus latomorum ichnogen. et ichnosp. nov.
and *Skartopus australis* ichnogen. et ichnosp. nov.

FIGURE A: *Wintonopus latomorum,* holotype (QM F10319). A right footprint preserved as natural mould, × 1. Lighting from NE. Attributed to an ornithopod dinosaur.

FIGURES B and C: *Skartopus australis,* holotype (QM F10330). A right footprint preserved as natural mould, × 1. In Fig. B lighting is diffuse, from above; in Fig. C lighting is from E. Attributed to a small theropod dinosaur (coelurosaur).


A
B
C

PLATE 8

Wintonopus latomorum ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURE A: Right footprint, × 0.5. Lighting from E. Showing pronounced anterolateral scrape-mark from digit 3, and a shorter scrape-mark from digit 4. No trace of interdigital web between digits 2 and 3. (QM F10322/II).

FIGURE B: Left footprint, × 0.5. Lighting from NE. Footprint foreshortened by toes entering and leaving sediment at steep angle. Interdigital web is clearly imprinted between digits 3 and 4, faintly imprinted between digits 2 and 3. Note backwardly-directed scrape-marks from digits 3 and 4. (QM F10322/II).

FIGURE C: Left footprint, × 0.5. Lighting from NE. Digit 2 contains raised 'cusp' formed by sediment adhering to underside of track-maker's toe. Footprint has poorly defined outline because it was badly damaged during excavation. (QM F10322/B).

FIGURE D: Left footprint, × 0.5. Lighting from SE. Anterolateral scrape-mark produces forked or Y-shaped outline to digit 3. Interdigital web is clearly imprinted between digits 3 and 4, absent between digits 2 and 3. (QM F10322/II).

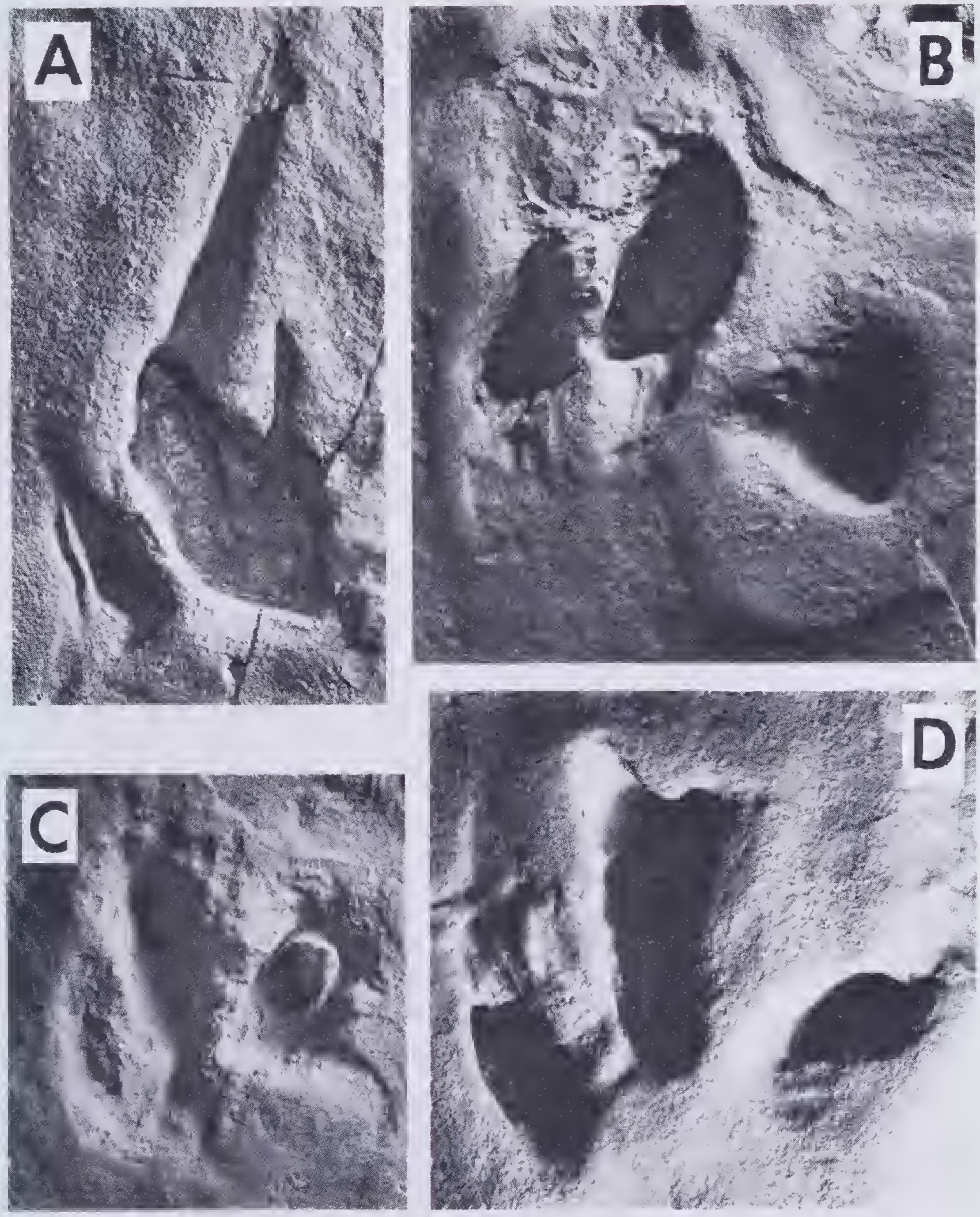

A
B
C
D

PLATE 9

Wintonopus latomorum ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURE A: Left footprint, × 1. Lighting from E. Shallow imprint with digit 2 exceptionally broad, and digit 4 represented by a furrow. Probably formed with the track-maker's body weight carried mainly on the two inner toes. (QM F10322/B).

FIGURE B: ?Right footprint, × 0.75. Lighting from E. Showing backwardly-directed scrape-marks from all three digits. (QM F10322/A).

FIGURE C: Right footprint, × 1. Lighting from NW. From the smallest trackway referred to *W. latomorum.* Note the distinct 'spur' behind digit 4, and the faint indication of an anterolateral scrape-mark from digit 3. (QM F10322/B).

FIGURE D: Right footprint, × 0.75. Lighting from N. From the second-largest trackway referred to *W. latomorum.* (QM F10322/1).

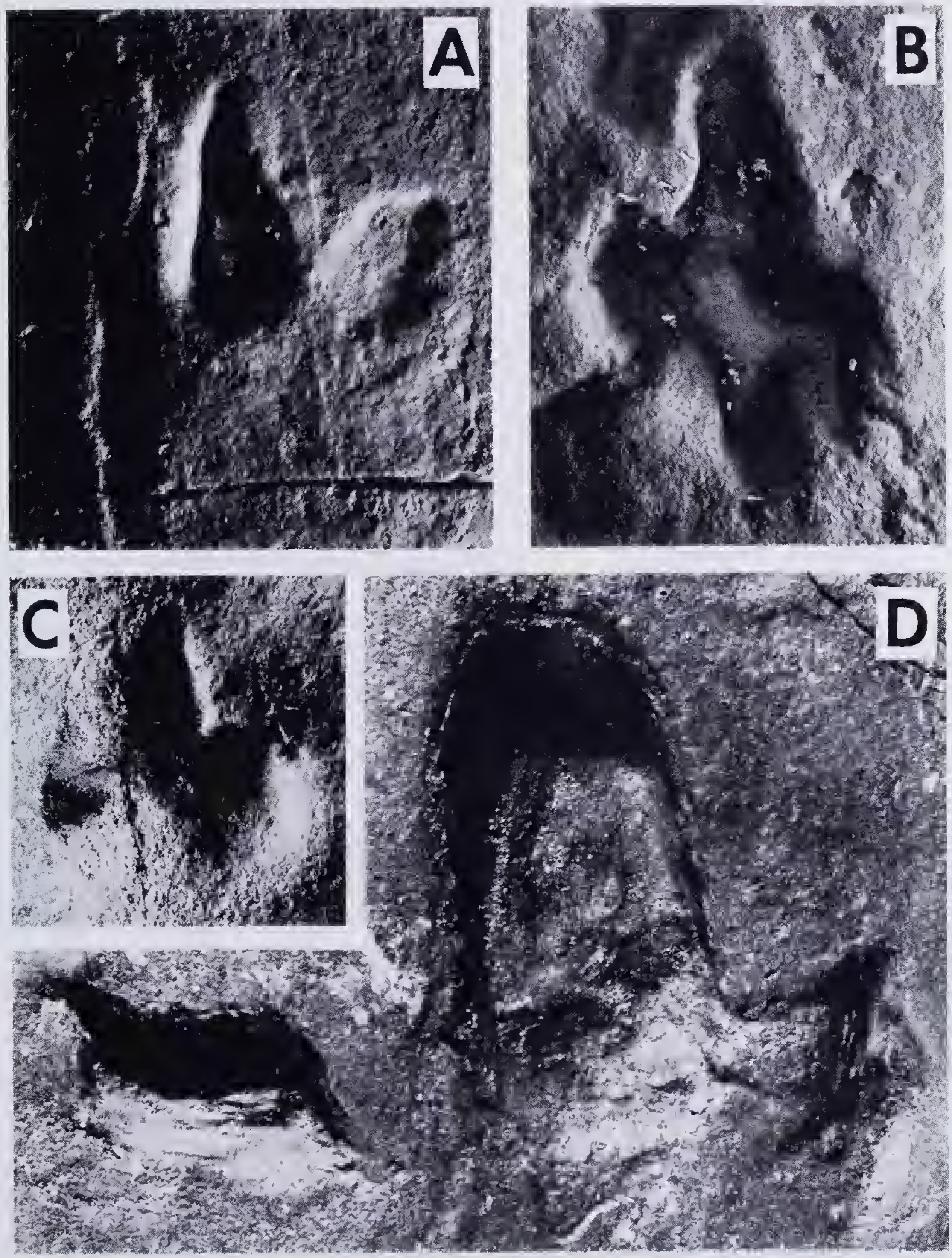

A
B
C
D

PLATE 10

Wintonopus latomorum ichnogen. et ichnosp. nov.,
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURE A: *Wintonopus latomorum;* left footprint, × 0.75. Lighting from NW. With all three digits represented by furrows, and with distinct trace of interdigital web between digits 3 and 4. There may also be a very faint imprint of the metapodium. (QM F10322/A).

FIGURE B: *Skartopus australis;* ?right footprint, × 0.66. Lighting from W. Characteristically divergent digits, but one of them (?2) unusually exaggerated in width. Presumably formed with track-maker's body weight carried mainly on the two inner toes. (QM F10322/B).

FIGURE C: *Wintonopus latomorum;* two right footprints, × 1. Lighting from NE. The slightly larger print (below) is fore-shortened by toes entering the sediment at a very steep angle. As toes were withdrawn the central one scraped the sediment forwards — so that it folded over to conceal digit 4 of a smaller and earlier-formed print. (QM F10322/II).

FIGURE D: *Wintonopus latomorum;* left footprint, × 0.33. Lighting from E. Showing exceptionally broad imprint of digit 3, and forwardly directed scrape-marks from all three digits. The scrape-mark from digit 3 is extremely long and is deflected slightly as it runs through the earlier-formed footprint of a coelurosaur (*Skartopus australis*). (QM F10322/II).

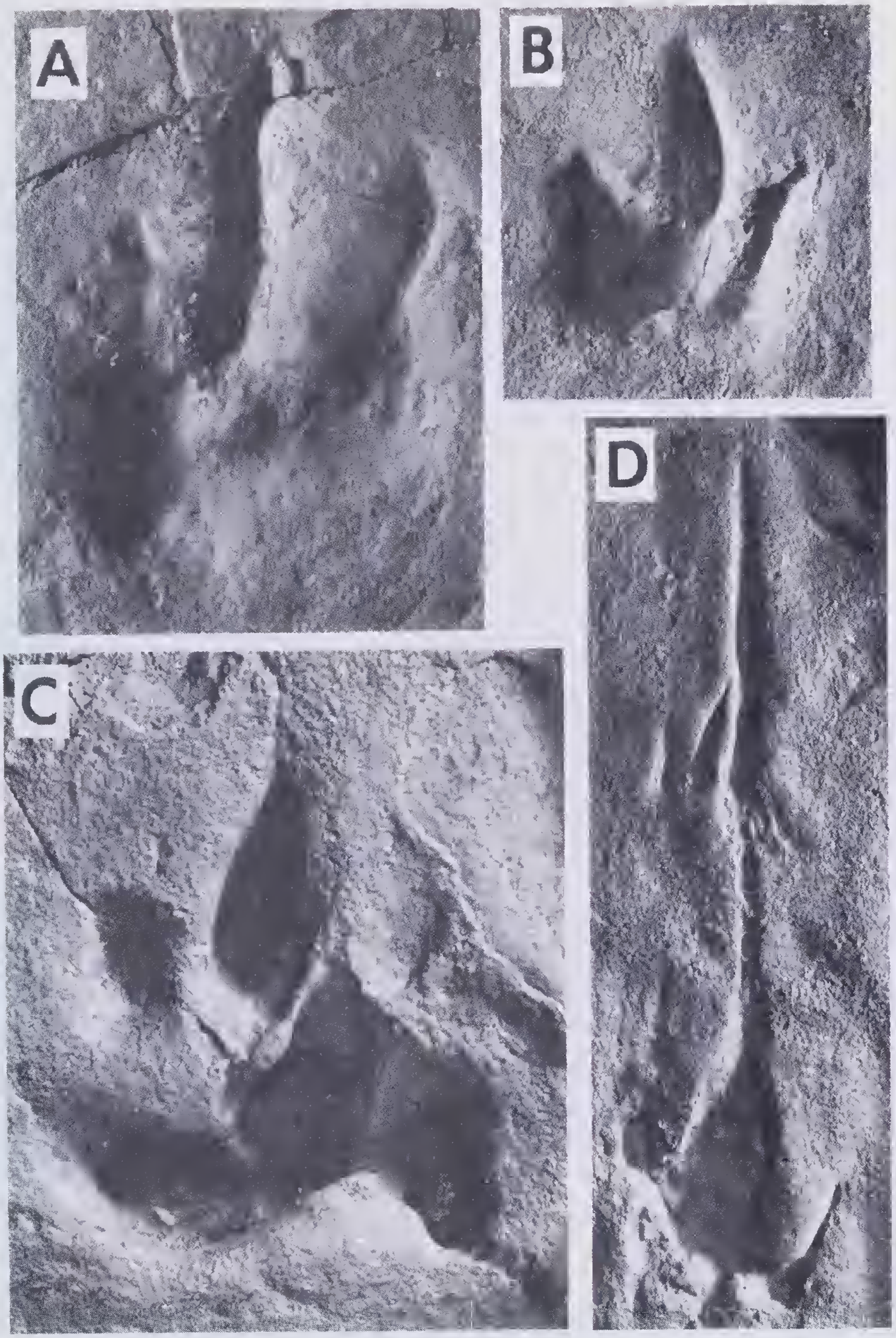

A
B
C
D

PLATE 11

Wintonopus latomorum ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry.

FIGURE A: Left footprint, × 1. Lighting from NE. Note deeply imprinted interdigital webs, and distinct curvature of digit 3. Photographed from rock slab (QM F10320).

FIGURE B: ?Left footprint, × 1. Lighting from N. Extremely fore-shortened on account of toes entering and leaving sediment at a very steep angle. Trace of posterior 'spur' at left (behind digit ?4) seems to confirm identification as left footprint. Fibreglass replica (QM F10322/I1).

FIGURE C: ?Left footprint, × 1. Lighting from SE. Three small pits seem to indicate brief touch-down of toe-tips after they had been withdrawn from the footprint. Location of these pits indicates that the foot was shifted forwards and slightly to the right, and that it was rotated around the axis of digit 3. Fibreglass replica (QM F10322/I1).

FIGURE D: Three left footprints (representing three track-makers), × 1. Lighting from W. All three examples show characteristic 'spur' behind digit 4. Uppermost example is very fore-shortened, with shallow imprint of digit 2; imprints of digits 3 and 4 are amalgamated. Lowermost example (bisected by joint) shows Y-shaped tip to digit 3. Fibreglass replica (QM F10322).

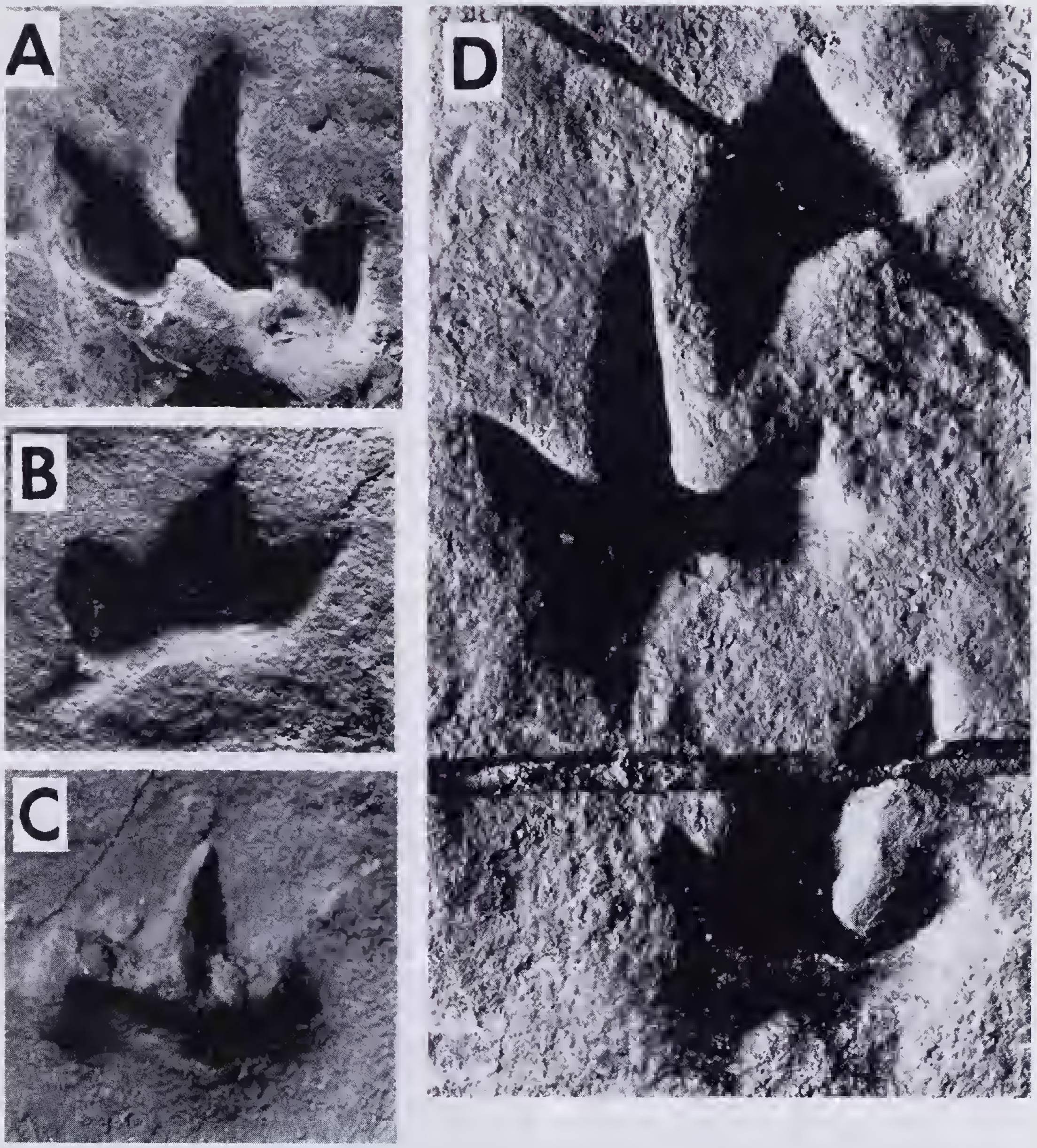

A
B
C
D

PLATE 12

Skartopus australis ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURES A and B: Single right footprint, × 1. In A lighting is from the NE, in B lighting is from the E. Showing full imprint of the metapodium. Note sharply pointed tips of digits (QM F10322/I).

FIGURE C: ?Right footprint, × 1. Lighting from NE. Somewhat fore-shortened, and with deeply incised scratches formed by backwards sweep of the track-maker's foot. (QM F10322/B).

FIGURE D: Right footprint, × 1. Lighting from E. Characteristic symmetrical arrangement of narrow and sharply pointed digits. Showing faint imprint of metapodium, traces of interdigital webs, and scratch-marks behind digits. (QM F10322/II).

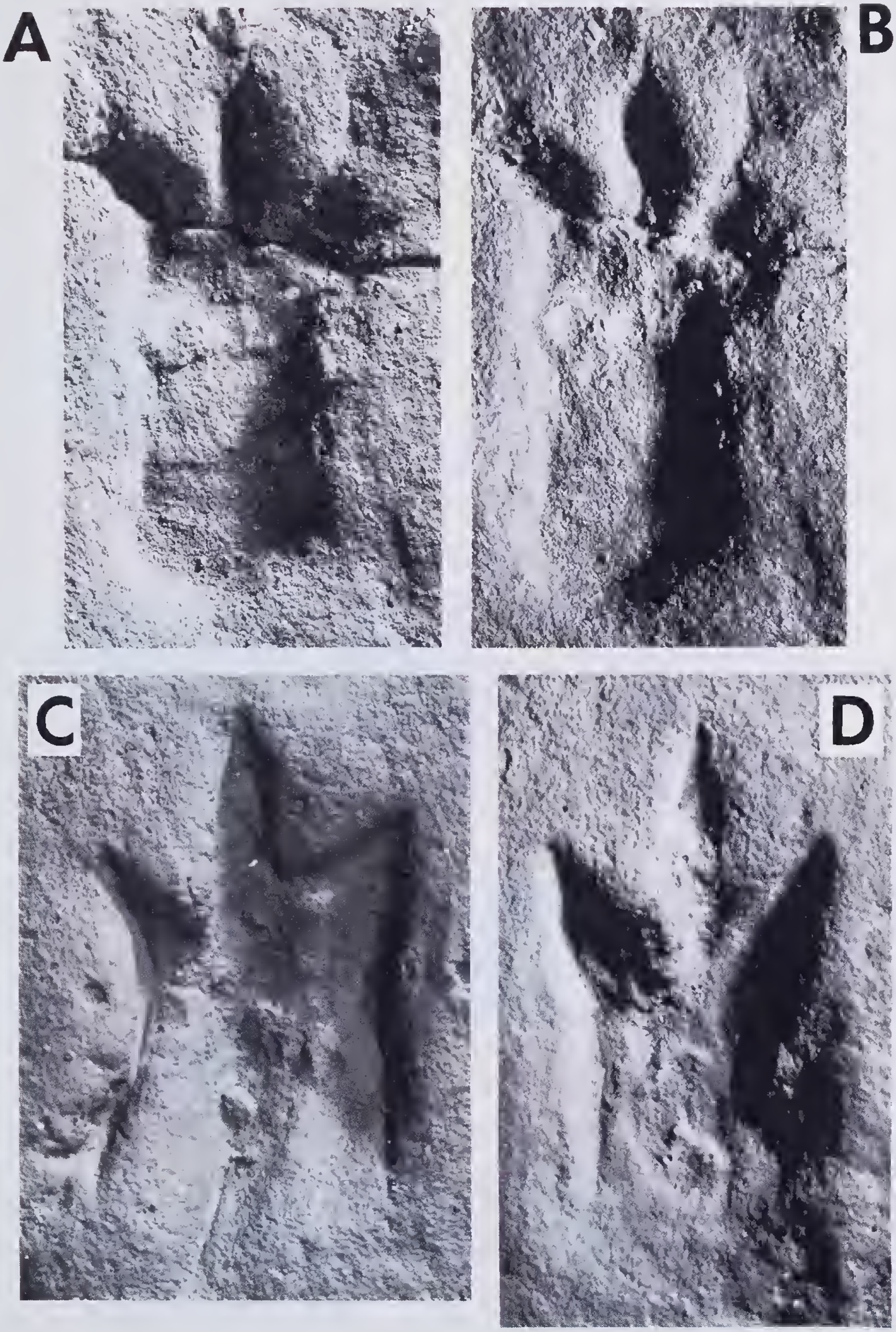

A
B
C
D

PLATE 13

Wintonopus latomorum ichnogen. et ichnosp. nov.,
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURE A: *Skartopus australis;* ?left footprint, × 0.66. Lighting from SW. Showing deeply incised scratch in the floor of each digit imprint. (QM F10322/B).

FIGURE B: *Skartopus australis;* ?left footprint, × 0.5. Lighting from N. Much fore-shortened example with imprint of metapodium. Fore-shortening accounts for apparently unusual thickness and bluntness of digit imprints (QM F10322/B).

FIGURE C: An amalgam of at least four footprints, × 0.66. Lighting from NW. Two outer digits of a left ornithopod footprint (*Wintonopus latomorum*) are visible at left, with a forwardly directed scrape-mark from digit 3. Note that all footprints are similar in depth, in state of preservation, and in orientation. (QM F10322).

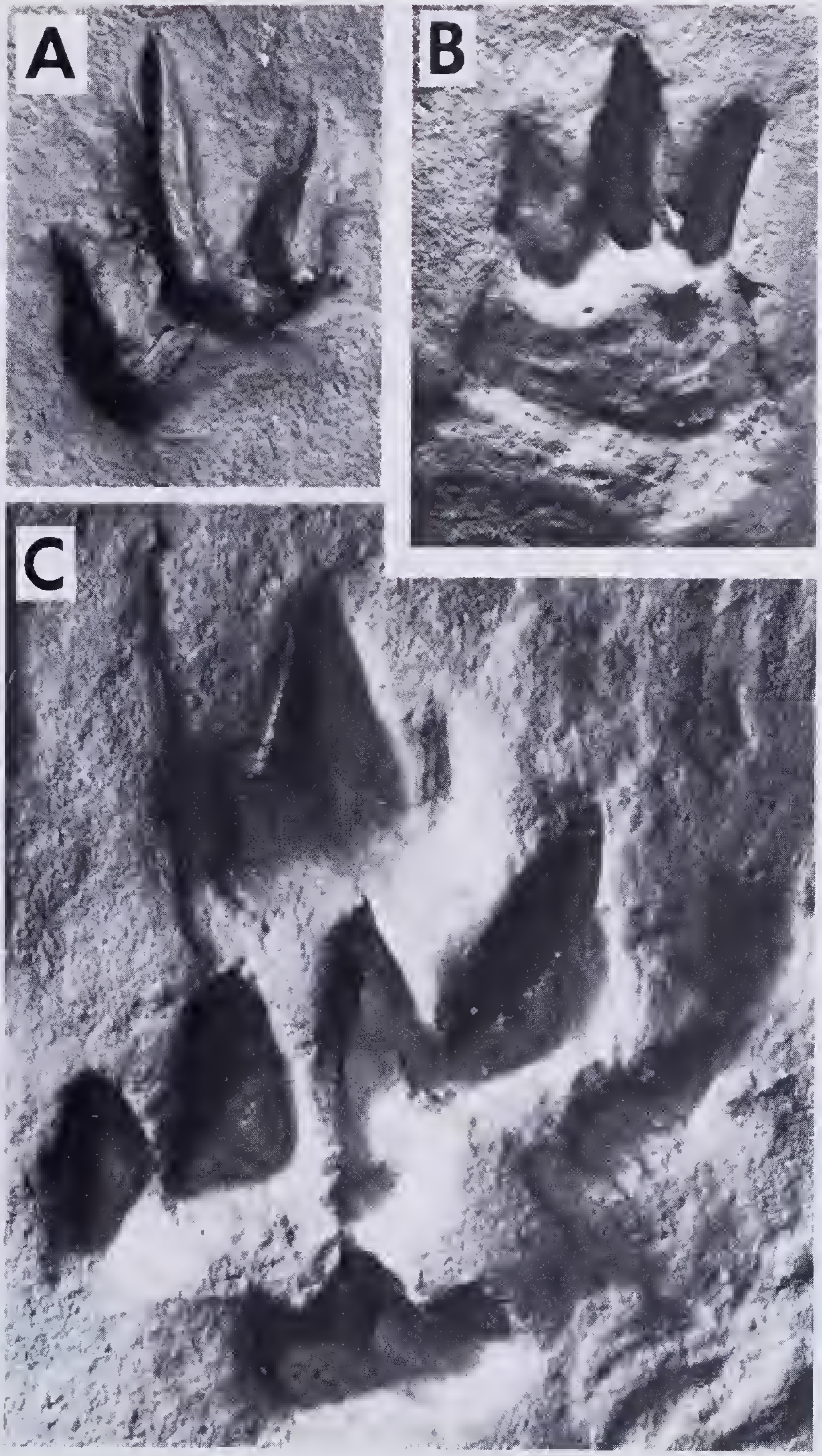

A
B
C

PLATE 14

Wintonopus latomorum ichnogen. et ichnosp. nov.,
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURE A: Group of three footprints (representing three animals), × 0.66. Lighting from SW. At top is a right footprint referred to *Wintonopus latomorum;* this shows exaggerated imprint of digit 2, and was presumably formed with track-maker's body weight carried mainly on the inner side of the foot. At centre is a footprint comprising three long scratches — probably from the left foot of a *Wintonopus* track-maker. Spacing of the three scratches would correspond to spacing of three digits in a left footprint of *Wintonopus* type. At bottom left is a ?right footprint referred to *Skartopus australis.* (QM F10322/B).

FIGURE B: Portion of Lark Quarry bedding plane, × 0.175. Lighting from S. Three footprints connected by lines are referred to *Skartopus australis* and form part of a single trackway. All three footprints (and two others not shown) have traces of the metapodium. Despite its 'flat-footed' gait this animal seems to have kept pace with other track-makers at Lark Quarry (see estimates of speed in Table 5). (QM F10322/B).


A
B

PLATE 15

Wintonopus latomorum ichnogen. et ichnosp. nov.,
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry.

FIGURE A: *Skartopus australis;* ?right footprint, × 1. Lighting from W. Note sharply pointed digits. Fibreglass replica (QM F10322/II).

FIGURE B: *Wintonopus latomorum;* left footprint, × 0.5. Lighting from NE. Showing characteristic proportions and spacing of the digits; note very slight curvature of digit 3. The outer side of the track-maker's foot (digit 4) was much more deeply impressed than the inner side (digit 2). Photographed from rock slab (QM F10320).

FIGURE C: A mixture of at least three footprints (representing at least three animals), × 1. Lighting from N. Apparently one example of *Wintonopus latomorum* is superimposed obliquely on another. The line of three puncture-like marks (top left) is a smaller and extremely fore-shortened footprint — formed by the track-maker's toes entering the sediment vertically. Photographed from rock slab (QM F10320).

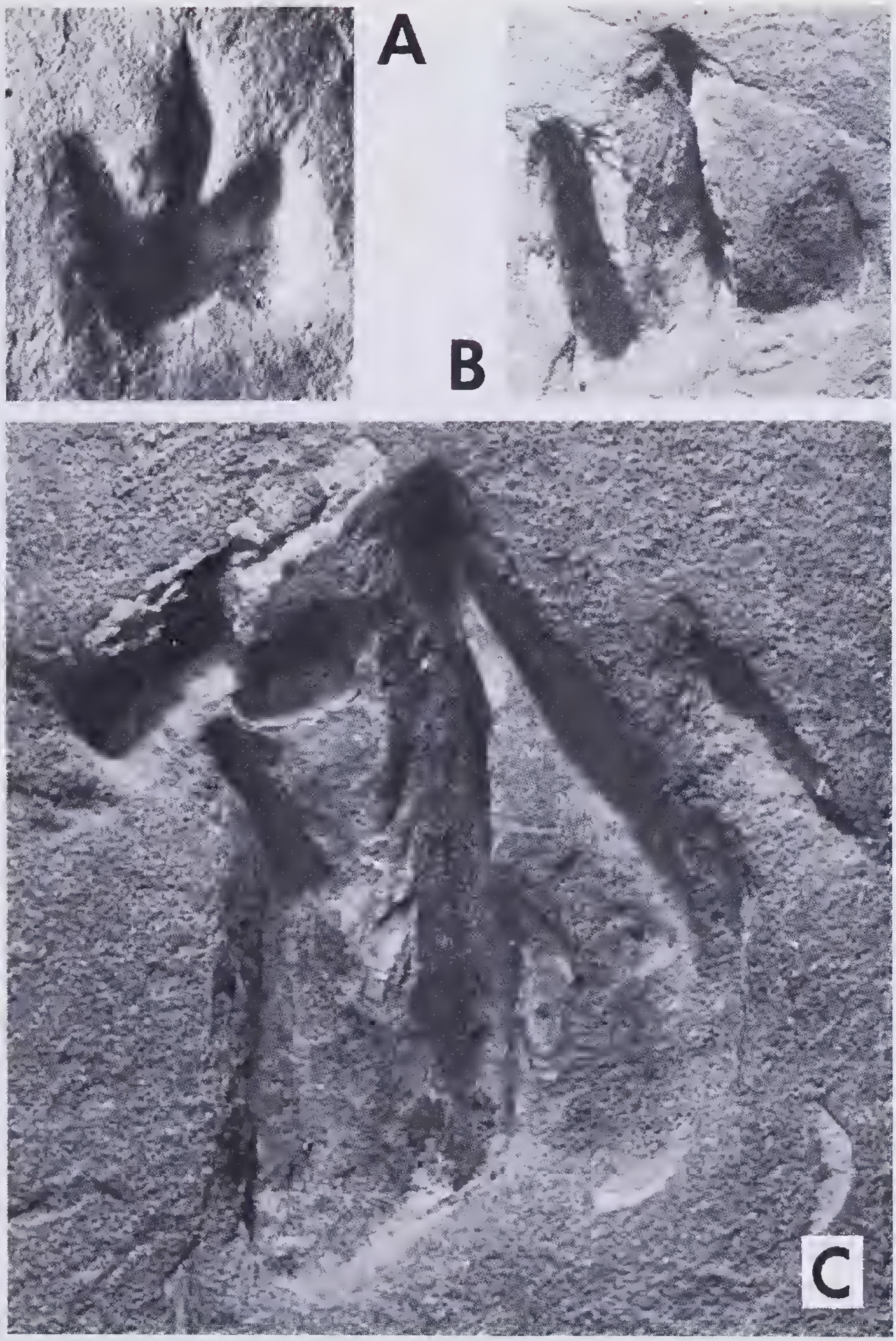

A
B
C

PLATE 16

Wintonopus latomorum ichnogen. et ichnosp. nov.,
and *Skartopus australis* ichnogen. et ichnosp. nov.

Referred specimens, all preserved as natural moulds at Lark Quarry, and all photographed from fibreglass replicas.

FIGURE A: *Skartopus australis;* left footprint, × 0.66. Lighting from SE. All three digits represented by scratches; note characteristic divergence of the digits (QM F10322/B).

FIGURE B: A group of between 6 and 8 footprints, × 0.5. Lighting from W. At lower left is an example of *Wintonopus latomorum* (somewhat damaged during excavation); at top right is a second example showing characteristic Y-shaped tip to digit 3. This second example has largely obliterated an earlier-formed footprint (to right), and is in turn partly distorted by a later-formed print (to left). At centre is a little-distorted example of *Skartopus australis.* Towards bottom right is a complete amalgam of at least two unidentifiable footprints (QM F10322/B).

FIGURE C: Three footprints (representing three animals), × 1. Lighting from W. A footprint at lower right (*?Skartopus*) is extended into anterior scrape-marks which partly disrupt two earlier-formed footprints. At lower left is a very characteristic example of *Wintonopus latomorum* (left footprint); at upper right is a smaller example (?right footprint). (QM F10322/A).

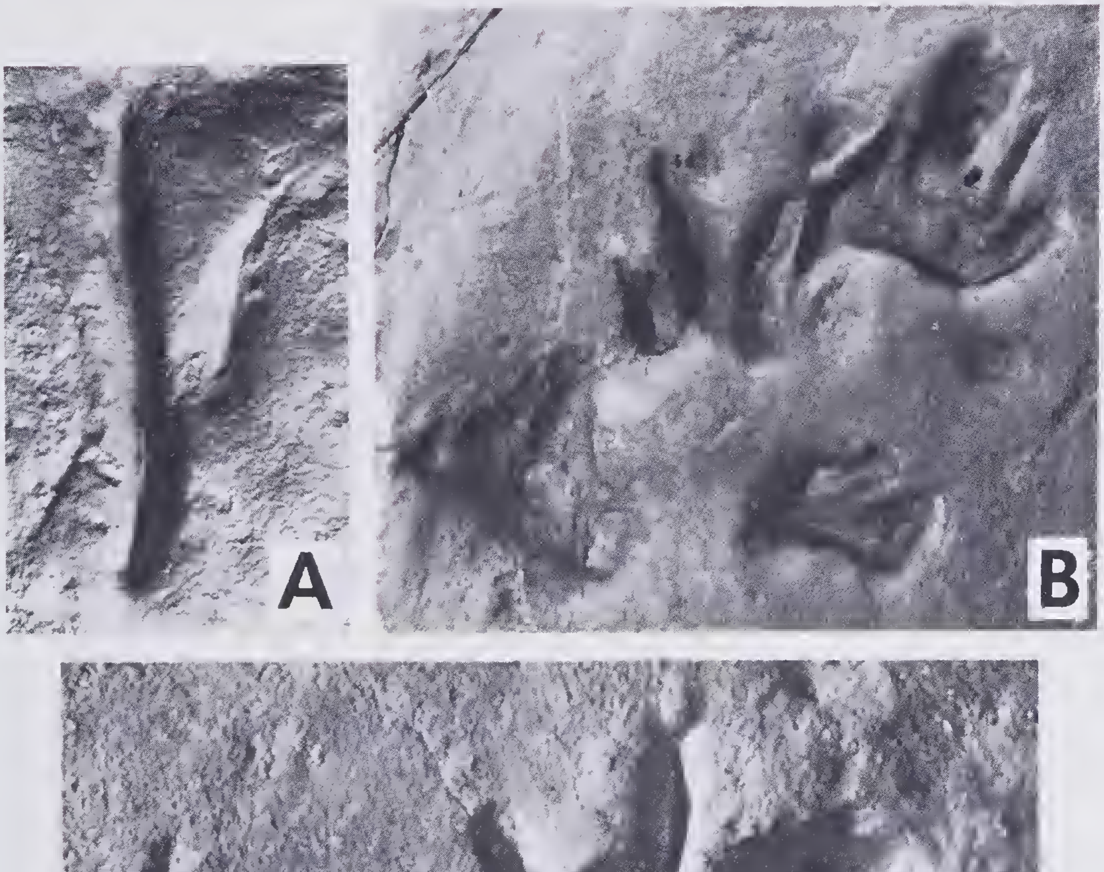

A
B
C

PLATE 17

Plan of footprints at Lark Quarry. Arrow indicates north.


N